Climate change can cause complex responses in Baltic Sea macroalgae : A systematic review

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Abstract

Estuarine macroalgae are important primary producers in aquatic ecosystems, and often foundation species providing structurally complex habitat. Climate change alters many abiotic factors that affect their long-term persistence and distribution. Here, we review the existing scientific literature on the tolerance of key macroalgal species in the Baltic Sea, the world's largest brackish water body. Elevated temperature is expected to intensify coastal eutrophication, further promoting growth of opportunistic, filamentous species, especially green algae, which are often species associated with intensive filamentous algal blooms. Declining salinities will push the distributions of marine species towards south, which may alter the Baltic Sea community compositions towards a more limnic state. Together with increasing eutrophication trends this may cause losses in marine-originating foundation species such as *Fucus*, causing severe biodiversity impacts. Experimental results on ocean acidification effects on macroalgae are mixed, with only few studies conducted in the Baltic

28 Sea. We conclude that climate change can alter the structure and functioning of macroalgal
29 ecosystems especially in the northern Baltic coastal areas, and can potentially act synergistically
30 with eutrophication. We briefly discuss potential adaptation measures.

31

32 **1 Introduction: Climate change impacts in marine ecosystems**

33 In the recent decade anthropogenic climate change has been recognized as a global biodiversity
34 threat, motivating extensive research on its biological impacts (Wernberg et al., 2012). However,
35 the majority of research has focused on terrestrial ecosystems, and detailed knowledge of impacts
36 in marine ecosystems is lagging behind (Rosenzweig et al., 2008).

37 Coastal macroalgae are important foundation species providing biomass and structurally complex
38 habitats important for coastal biodiversity (Airoldi et al., 2008; Eriksson et al., 2006). Macrolgal beds
39 are highly productive environments comprising an important carbon sink (Chung et al., 2011).
40 Climate change has caused extensive poleward shifts of macroalgal distributions including range
41 contractions as species are tracking their thermal niches (Nicastro et al., 2013; Wernberg et al.,
42 2011), and more extensive shifts have been projected for the future (Jueterbock et al., 2013; Müller
43 et al., 2009). Macroalgae have been proposed to benefit from ocean acidification (OA) (Hall-Spencer
44 et al., 2008; Koch et al., 2013) but so far experimental evidence remains mixed (Hurd et al., 2009).

45 In this study we review climate change impacts on key Baltic Sea macroalgae species. As shallow
46 inland sea, the Baltic is particularly prone to warming, and observed rates of warming at the end of
47 the 20th century have been highest in all of the world's large marine ecosystems (Belkin, 2009). We
48 utilize both studies that have been conducted with climate change focus, as well as studies that
49 have been conducted on environmental tolerances of key species.

The Baltic Sea is a large, shallow brackish water epeiric sea heavily impacted by human activities. Allegedly one of the biggest threats to the Baltic ecosystem during the 21st century is climate change with predicted declines in salinity and elevated temperatures (Meier et al., 2012a). As the brackish water environment is challenging for both marine and limnic species, the Baltic Sea ecosystem is relatively species-poor, and the species distributions are controlled by a steep salinity gradient. Low salinity and seasonal temperature oscillations cause many species to exist at the edges of their geographic distribution (Hällfors et al., 1981), and towards the northern areas in the Baltic Sea the conditions become more severe in form of shorter growing season, longer ice cover, and declining salinity (Fig. 1a).

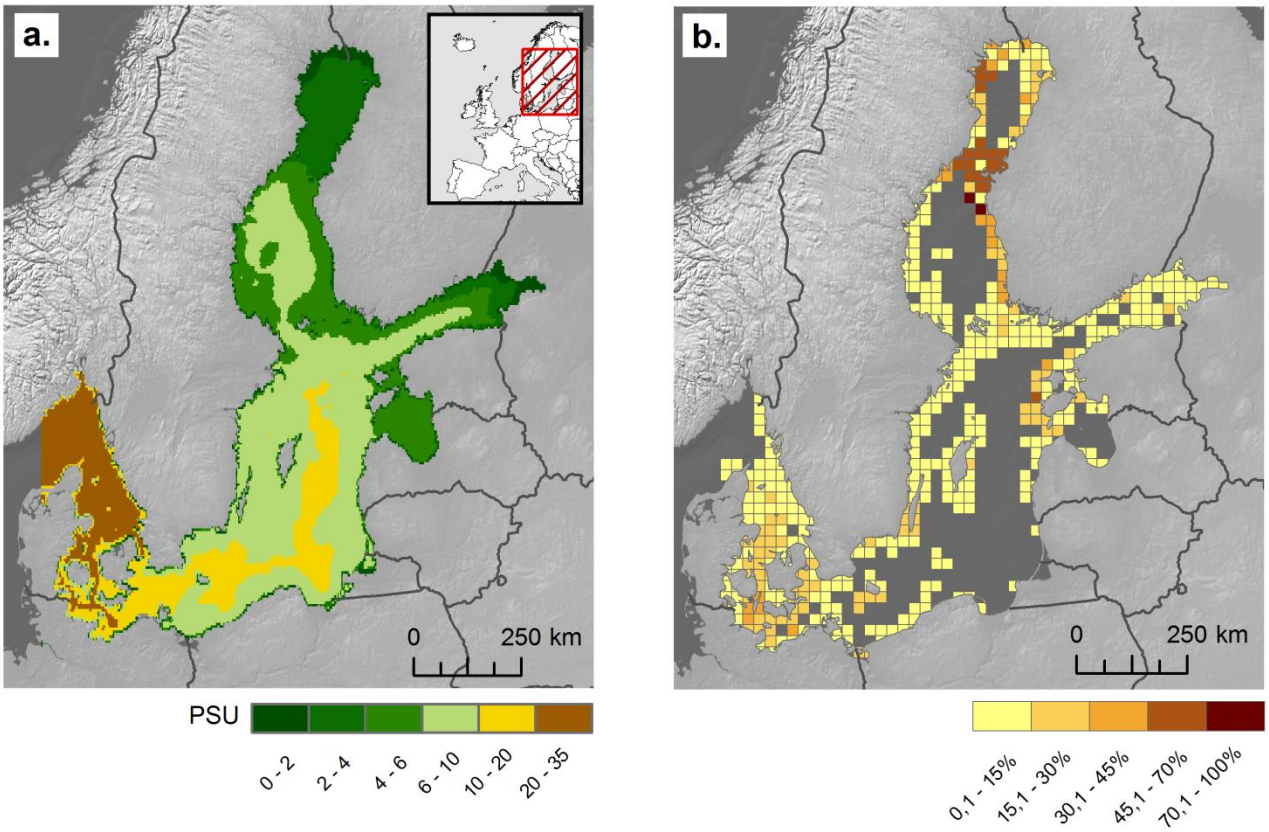


Fig. 1 a) Current salinity distribution of the Baltic Sea b) abundance of photic hard bottoms, the potential habitat for the macroalgae. Values are percentages of photic hard bottoms in relation to total bottom area. Data source: a) EUSeaMap (Cameron and Askew, 2011) b) Benthic biotope complexes in the Baltic Sea (HELCOM, 2010).

In the Baltic coastal zones, the habitat-forming macroalgae are the foundation species in rocky shore ecosystems, which are the prevalent shore types in the northern and western archipelago areas (Hällfors et al. 1981, Fig. 1b). The vertical zonation of algal species creates a structurally complex habitat, which is important for both juvenile fish and small invertebrates, thus harboring a large fraction of biodiversity in the Baltic coastal ecosystems (Hällfors et al., 1981; Kautsky et al., 1992). Especially the perennial, habitat-forming species have suffered from coastal eutrophication, causing declines in abundance and depth penetration during the 20th century (Kautsky and Kautsky, 1986). Eutrophication has also favoured fast-growing, filamentous species, which has culminated in the emergence of drifting, decomposing algal mats destroying soft-bottom communities (Norkko and Bonsdorff, 1996).

While in oceanic areas climate change has been projected to cause northward shifts in macroalgal distributions (Müller et al., 2009), the patterns are different in the Baltic. Declining salinities (Meier et al., 2012a) may counteract the general trends, pushing the distributions of marine-originated species towards south (Vuorinen et al., 2015). This, together with other interacting human impacts makes the Baltic macroalgae particularly interesting study organisms for climate change ecology. As the northern and western shores and archipelagos of the Baltic contain large fraction of the suitable shores for macroalgae, we focus our review on dominant species occurring in these areas.

2 The changing abiotic conditions in the Baltic Sea

The sea surface temperature (SST) of the Baltic has warmed rapidly during recent decades. Siegel *et al.* (2006) observed warming of 0.8 ^{o}C over 15 years, in good agreement of unprecedented

warming of 0.6 °C between 1985 and early 2000 reported by MacKenzie & Schiedek (2007), who also reported increased frequency of extreme temperatures. MacKenzie & Schiedek (2007) observed the warming of the Baltic and North Sea to be three times higher than the global average. The BACC I report (BACC Author Team, 2008) states warming of air temperatures by 1 °C from the beginning of the 1980s to 2004, while Lehmann *et al.* (2011) identified warming of 0.5 °C per decade for the northern Baltic, which seems to be warming more rapidly. Finally, Belkin (2009) reported observed warming of SST of 1.35 °C (1982-2006), which was higher than in any other Large Marine Ecosystem in the world, and seven times higher than the observed global warming rate (Belkin, 2009).

Salinity conditions in the Baltic depend on riverine inflow of fresh water and stochastic inflow of saline water through Danish straits (Leppäranta and Myrberg, 2009). No clear long-term trend in salinity has been observed for the last hundred years (Fonselius and Valderrama, 2003; Winsor et al., 2001), although large decadal oscillations exist. However, the salinity change from external forcing would expectedly be slower than temperature change because of latency related to water-exchange (Myrberg et al., 2006). Nutrient concentrations have increased notably over the 20th century as a consequence of increased anthropogenic emissions (Fonselius and Valderrama, 2003), and have contributed substantially to the present-day seasonal pH oscillations (Omstedt et al., 2009).

The eventual impacts of climate change in the Baltic will depend on a multitude of factors, including the realized emissions, sensitivity of climate system to greenhouse gas emissions, stochastic regional climate as well as interactions with other anthropogenic drivers, such as eutrophication. On a broad scale, the mean annual sea surface temperatures of the Baltic have been projected to increase by 2 to 4 °C by the end of century. Higher temperature increases (4 °C) have been projected

for the northern areas such as Bothnian Bay, and more moderate increases (2 ^{o}C) for southern areas (HELCOM, 2013).

Warming is expected to promote an increased frequency of short-term extreme heat events near the surface (MacKenzie and Schiedek, 2007; Neumann et al., 2012). Currently, sea ice lasts for 5 to 7 months in the northern parts of the Baltic, and during very cold winters, the entire Baltic can freeze over (Leppäranta and Myrberg, 2009). Winter-time warming can cause a 60-80 % reduction in the duration of sea ice by the end of the century (Meier, 2006; Neumann, 2010), promoting longer growing season and increased light availability. Elevated temperatures increase respiration and together with consequent increases in primary production may cause increased frequencies of anoxia (Neumann et al., 2012), which promotes release of mineralized nutrients from the sediments, intensifying eutrophication further (Meier et al. 2012c; Neumann et al. 2012).

The salinity of the Baltic has been projected to decline by 2 to 3 units by the end of the century, caused by increased fresh-water runoff (Meier 2006), however, there is large uncertainty related to the accuracy of salinity projections (HELCOM, 2013; Leppäranta and Myrberg, 2009; Meier, 2006; Meier et al., 2006). Declining salinity decreases stratification, which slightly improves oxygen conditions in suboxic areas, however, on average the future bottom oxygen conditions are expected to deteriorate (Neumann 2010; Meier et al. 2012c).

In most parts of the Baltic, increased river inflow causes increased nutrient and organic carbon input (Meier, 2006; Meier et al., 2012b), leading to increased nutrient loading, especially in winter, when biological nutrient uptake is absent. Also the remobilization of nutrients stored in the sediments has been predicted to increase as a consequence of elevated temperatures (Meier et al. 2012b, 2012c). However, in the Bothnian Bay, the increased precipitation may lead to more oligotrophic conditions (HELCOM, 2013). The future nutrient loading will depend also on agricultural policy and

130 the intensity of agriculture in the drainage area, and the policies applied for nutrient emission
131 reductions (Meier et al., 2012c; Seitzinger et al., 2002). The wintertime river inflow will increase in
132 the north coupled with lower and earlier springtime peak flows, which may alter the temporal
133 salinity patterns (BACC Author Team, 2008). The intensity of springtime river flows has been
134 predicted to decrease with declining snow cover, which will also cause the peak freshwater inflow
135 to shift earlier in many areas (HELCOM, 2013).

136 Globally, the mean pH of sea water is predicted to decline by 0.3 - 0.4 units towards the end of the
137 century unless the global CO_2 emissions are controlled (Feely et al., 2009). The Baltic ecosystem is
138 especially vulnerable to acidification because of the low buffering capacity of brackish water
139 (Omstedt et al., 2010), the high freshwater input with high levels of dissolved organic carbon (DOC)
140 and low alkalinity (caused by low pH soils in the drainage area) (Omstedt et al., 2010). In the Baltic,
141 the mean pH levels have been estimated to decline by 0.25-0.34 units by the end of the century
142 (Kuznetsov and Neumann, 2013; Omstedt et al., 2010). However, on average these declines are
143 smaller than the current annual pH oscillations between summer and winter (Omstedt et al., 2010;
144 Saderne et al., 2013), and they are damped by large diurnal oscillations, which may exceed 1 unit
145 in highly productive ecosystems such as macroalgal beds (Middelboe and Hansen, 2007).

146 The acidification in the Baltic is strongly linked to nutrient emissions. If eutrophication continues,
147 also the annual oscillations will intensify in the future as carbon is taken up by primary producers
148 during the summer, and again released during the winter (Omstedt et al., 2010), resulting in more
149 frequent periods of low pH. Additional input of organic carbon through increased riverine flow may
150 further intensify these trends (Omstedt et al., 2010).

151 Acidification and elevated atmospheric CO_2 increases the concentrations of dissolved inorganic
152 carbon (DIC), and changes the relative abundances of DIC components: increased levels of dissolved

153 aquatic CO_2 and bicarbonate (HCO_3^-), and reduced levels of carbonate (CO_3^{2-}). The highest relative
154 increase will be in CO_2, which will increase by 250 % if atmospheric CO_2 rises to 1000 ppm (Koch et
155 al., 2013). This will change the carbon availability for photoautotrophs, and may potentially elevate
156 marine primary production (Hurd et al., 2009; Koch et al., 2013).

157

158 **3 Macroalgae in the Baltic Sea**

159 The Baltic macroalgal community is characterized by a salinity gradient imposing restrictions on
160 species occurrences and importance of few perennial habitat-forming species such as *Fucus* spp.
161 and *Furcellaria lumricalis*. As these characteristics of the ecosystem have been covered in earlier
162 studies (e.g. already by Waern (1952), we do not describe them in detail here but briefly summarize
163 the main features (Table 1).

164

165 Table 1. Main characteristics of macroalgal community of the Baltic

Macroalgae of the Baltic Sea

- Total 442 macroalgae species observed (Nielsen et al., 1995)
- The majority of species have colonized Baltic from the Atlantic and have adapted to low salinity (Bäck et al., 1992; Russell, 1985)
- Biota controlled by salinity gradient, and the number of macroalgae species declines with salinity (Nielsen et al., 1995; Waern, 1952)
- Fucoids most important habitat-forming species in Baltic Proper (Kautsky et al., 1992; Malm et al., 2001)
- *Fucus vesiculosus* is the main habitat-forming species with 90 % of plant biomass in hard bottoms (Kautsky and Van der Maarel, 1990)
- In eastern and southern shores *Furcellaria lumbricalis* forms important habitats (Bučas et al., 2007)
- Filamentous algae are major seasonal primary producers with peak abundances in summer (Kautsky, 1995; Kiirikki and Lehvo, 1997)
- Eutrophication has caused extensive blooms of filamentous algae and declines in abundance an depth penetration of habitat-forming species such as fucoids (Kautsky and Kautsky, 1986; Lehvo and Bäck, 2001)

166

167 **4. Methods**

168 We selected the species from distributional indexing of Nielsen *et al.*, (1995) from areas with indexes
169 from 4 to 10, consisting of Baltic Proper, Gotland Sea, Estonian coast, Gulf of Finland, Archipelago
170 Sea, Åland Sea and Gulf of Bothnia. As we wanted to focus only on the most ecologically significant
171 species, we selected species that were classified by Nielsen *et al.*, (1995) as "dominant" in any of
172 these areas or "frequent" in most areas. We added to this species list two species frequent in the
173 least saline areas (*Cladophora aegagropila* and *Cladophora fracta*), yielding a total 31 species; 8
174 from bangiopheceae, 11 fucophyceae, and 12 chlorophyceae (Table 2). Also *Fucus radicans* was
175 added into the species search list as this species was only relatively recently identified as species
176 (Bergström et al., 2005) and thus not included in the indexing of *Nielsen et al.* (1995).

177 We searched ISI Web of Knowledge for scientific articles with species scientific name together
178 (operator "and") with following keywords: "temperature", "heat shock", "salinity", "osmotic stress",
179 "nutrients", "eutrophication" and "ocean acidification" from the topic field.

180 In addition, we performed a heuristic search with the same criteria using Google Scholar to provide
181 a quick comprehensive screening of the existing literature. If studies addressing the factors in
182 question were found with the study species, these were included even if the actual study had been
183 performed outside the Baltic.

184 We classified the responses of the species into four categories: "beneficial", "potentially beneficial",
185 "tolerant" and "harmful", respectively, for four abiotic variables: warming, declining salinity,
186 eutrophication, and ocean acidification. As the literature found contained reports of laboratory
187 experiments with various treatment levels, field manipulations as well as observations of species'
188 distributions, classification of the responses required some subjective consideration.

189 We used psu 4 as a threshold for salinity decline, as salinity of 5 psu has been identified to be critical
190 threshold for persistence of many marine species (Schubert et al., 2011; Vuorinen et al., 2015), thus
191 we examined the observed responses of the species for salinities under 4 psu. Negative
192 experimental responses (declines in photosynthesis, growth or survival) or field observations which
193 showed decline in abundance, biomass or reproduction when salinity declined under 4 psu, were
194 classified as "harmful". If no response against experimental manipulation, or no observed changes
195 in the field under 4 psu was found, the species was classified "tolerant". Positive experimental
196 responses or increasing abundance under declining salinity were classified as "beneficial".

197 Temperature responses were classified similarly, although here no exact temperature threshold for
198 "elevated" temperature was set. Declining growth or photosynthesis, increased mortality or
199 overgrowth by epiphytes observed in elevated temperature experiments were classified as

200 “harmful”. We also classified response as “harmful”, if the species had low thermal growth range or
201 low upper survival temperature limit, obtained through distribution observations and experiments,
202 sensu Wiencke et al. (1994), or if the observed abundance of the species in the field declined under
203 elevated temperature, for example under artificial heating. Response was classified “tolerant” if the
204 species showed no response in elevated temperature experiments, or had wide thermal growth
205 range, and high upper survival temperature, and no changes in abundance under elevated
206 temperature. “Beneficial” responses included positive experimental responses, high thermal growth
207 range, or positive changes in abundance when temperature was increased. In all temperature
208 classifications, we classified the responses considering the projected future temperatures in the
209 Northern Baltic.

210 “Harmful” responses to Ocean Acidification were cases of declining growth, photosynthesis or
211 increased photoinhibition in the laboratory, or decreased abundance under low pH condition in the
212 field. “Tolerant” responses were cases where no effects or changes in abundance were observed,
213 and “Beneficial” positive responses or increased abundance. OA was the only variable for which the
214 category “potentially beneficial” was used. In these cases, experimental responses indicated either
215 positive responses against OA treatment in only a particular season, positive photosynthesis
216 response when total inorganic carbon was increased, or indication of reliance on free CO_2 in carbon
217 acquisition, which could potentially lead to positive effects under elevated CO_2 levels (Koch et al.,
218 2013).

219 Responses to eutrophication were classified similarly as other variables. If a shift of macroalgal
220 zonation towards the surface or decreased depth penetration with increasing eutrophication was
221 observed, this was considered “harmful”, as were failures in germination or declining abundance in
222 eutrophic conditions. Species was considered “tolerant” against eutrophication, if no effects on

223 recruitment, growth or abundance were observed under eutrophication, and "beneficial" if the
224 abundance of the species increased under eutrophic conditions.

225

226 **5. Results - Impacts of climate change on Baltic macroalgae**

227 For the selected species, a total of 3042 papers were found from the Web of Knowledge. Of these,
228 128 papers contained information over the variables studied here (Table 2, Table S1). Here, a
229 summary of the responses is provided (Table 2), exact literature references for the responses are
230 given in supplementary material (Table S1).

231 Table 2. Responses of key macroalgal species to expected abiotic changes. Number of papers found relating to response
232 against each variable are given in parenthesis. Green indicates positive effects, gray neutral and red negative.

Species	***No of hits WoS***	***No of articles referred in here***	***Growth form***	***Warming***	***Declining salinity***	***Ocean acidification***	***Eutrophication***
RED ALGAE							
Hildenbrandia rubra	20	4	Perennial, encrusting	Tolerant (1)	Tolerant (3)	Beneficial (1)	
Coccotylus truncatus syn. *Phyllophora brodiaei*, *P. truncata*	23	4	Perennial, foliose	Beneficial (1)	Tolerant (1)	Potentially beneficial (1)	Tolerant (1)
Furcellaria lumbricalis	61	8	Perennial, dichotomous, corticated	Beneficial (2)	Harmful (3)	Beneficial (2)	Tolerant (2)
Ceramium tenuicorne	35	7	Annual, filamentous, partial cortication	Harmful (1)	Tolerant (5)		Beneficial (1) Harmful (1)
Ceramium virgatum syn. *C. rubrum, C. nodulosum*	24 59	0	Annual, filamentous, corticated				
Polysiphonia fucoides syn. *P. nigrescens*	22 7	4	Perennial, polysiphonous		Harmful (2)		Beneficial (1) Tolerant (1)
Polysiphonia fibrillosa syn. *P. violacea*	3 6	2	Annual, polysiphonous		Harmful (2)		
Rhodomela confervoides	73	4	Annual, corticated		Tolerant (2) Harmful (1)		Beneficial (1)
BROWN ALGAE							

Pylaiella littoralis often misspelled *Pilayella littoralis*	103 93	10	Annual, filamentous uniseriate	Harmful (2)	Tolerant (4)		Beneficial (4)
Ectocarpus siliculosus	342	10	Annual, filamentous uniseriate	Tolerant (2) Beneficial (1)	Tolerant (2) Harmful (1)		Beneficial (4)
Elachista fucicola	13	0	Annual, filamentous uniseriate				
Eudesme virescens	3	1		Beneficial (1)			
Pseudolithoderma spp.	11	0	Perennial, encrusting				
Dictyosiphon foeniculaceus	11	0	Cylindrical, branched thallus				
Stictyosiphon tortilis	2	1	Cylindrical, branched thallus				Harmful (1)
Scytosiphon lomentaria	130	4	Annual, tubular, often regular constrictions	Tolerant (3)	Tolerant (1)		
Chorda filum	33	3	Annual, strapshaped multicellular thallus	Tolerant (1) Harmful (1)	Tolerant (1)		
Fucus vesiculosus	1450	53	Perennial, multicellular thallus with differentiated cell structures	Beneficial (5) Harmful (8) Tolerant (1)	Tolerant (5) Harmful (3)	Tolerant (2) Potentially beneficial (2) Harmful (3)	Harmful (30)
Fucus radicans	11	2	Perennial, multicellular thallus with differentiated cell structures	Harmful (2)	Tolerant (1)		
GREEN ALGAE							
Ulva flexuosa syn. *Enteromorpha flexuosa*	9 18	6	Annual, tubular	Beneficial (3)	Tolerant (2)		Beneficial (3)
Ulva intestinalis syn. *Enteromorpha intestinalis*	24 90	26	Annual, tubular	Beneficial (6)	Tolerant (7) Harmful (1)	Beneficial (1)	Beneficial (11)
Ulva linza syn. *Enteromorpha ahleriana*	38 1	10	Annual, tubular	Beneficial (6) Tolerant (1)	Harmful (2) Tolerant (1)		Beneficial (2)
Ulva prolifera syn. *Enteromorpha prolifera*	99 71	11	Annual, tubular	Beneficial (2)	Tolerant (4)	Potentially beneficial (1) Harmful (1)	Beneficial (4)
Ulothrix subflaccida	1	3	Annual, filamentous uniseriate	Harmful (1)	Tolerant (2)		
Ulothrix zonata	11	0	Annual, filamentous uniseriate				

Monostroma grevillei syn. *Ulvopsis grevillei*	40	2	Annual, filamentous uniseriate	Harmful (2)	Harmful (1)	
Urospora penicilliformis	5	1	Annual, filamentous uniseriate		Tolerant (1)	
Cladophora aegagropila	3	1	Annual, filamentous uniseriate		Beneficial (1)	
Cladophora fracta	7	0	Annual, filamentous uniseriate			
Cladophora glomerata	112	15	Annual, filamentous uniseriate	Beneficial (6) Tolerant (2)	Beneficial (3) Tolerant (2) Harmful (1)	Beneficial (3)
Cladophora rupestris	22	3	Annual, filamentous uniseriate	Tolerant (1)	Harmful (2) Tolerant (1)	

5.1. Temperature and light: direct physiological effects

In oceans, temperature is one of the most important determinants for the geographic ranges of macroalgal species (Eggert, 2012), and elevated temperatures expectedly shift macroalgal distributions towards the poles (Jueterbock et al., 2013; Müller et al., 2009; Nicastro et al., 2013). However, in the Baltic Sea scale, species distributions are mainly controlled by salinity gradient (Eriksson and Bergström, 2005; Nielsen et al., 1995; Schubert et al., 2011), and thus the exact effects of temperature increases on species' distributions are hard to predict, although some studies suggest northward shift of fucoid distributions (Leidenberger and Giovanni, 2015). Elevated temperature has a direct control over many phenological processes. Increased temperature, in the form of mild winters, has been shown to accelerate receptacle growth of *F. vesiculosus,* causing earlier reproduction in the Baltic Sea (Kraufvelin et al., 2012). Ice-free winters may allow also the perennial species to grow in the filamentous algal zone near the surface, if disturbance from ice scraping is missing (Kiirikki, 1996). Temperature effects also depend on local habitat features and may be especially pronounced on e.g. sheltered sites (Gubelit, 2015).

Species living in areas with high seasonal temperature fluctuations (such as the Baltic) generally have a higher ability to acclimate to ambient temperature changes (Eggert, 2012). If the geographic distribution of the species covers a wide temperature gradient, intraspecific differences in optimal temperatures may also occur between local populations. Indeed, *F. radicans* has been shown to have higher sensitivity to short-term heat shocks than *F. vesiculosus* (Lago-Lestón et al., 2009), possibly as an indication of more cold-adapted physiology.

The exact thermal tolerances of Baltic macroalgae have not been widely studied, but many large macroalgal species in the North Sea have a broad temperature optima between 10 and 15 ^{o}C (Fortes and Lüning, 1980). Baltic *F. vesiculosus* has been found to have lower temperature optima for growth and photosynthesis than the Atlantic populations (Nygård and Dring, 2008). Moderate warming has been observed to increase the growth of *F. vesiculosus* (Al-Janabi et al., 2016a; Lehvo et al., 2001), however, even short exposures to temperatures higher than 27 ^{o}C are lethal for both juvenile and adult thalli (Al-Janabi et al., 2016a; Graiff et al., 2015).

Our literature review reveals that species that would benefit most from the warming are filamentous green algae, mainly *Ulva* spp. and *C. glomerata*. In addition, some positive responses were found for leathery red alga *Coccotylus truncatus*, as well as filamentous brown *Ectocarpus siliculosus* and *Eudesme virescens* (Table 2).

Few clearly cold-water species were identified, for which temperature increases may be harmful. These were the filamentous red alga *Ceramium tenuicorne*, filamentous brown alga *Pylaiella littoralis*, and green algae *Ulothrix subflaccida* and *Ulothrix grevillei* (Table 2), although in general, responses for warming in green algae were positive. Expected responses of *F. vesiculosus* were quite divergent, reflecting the difficulty of assessing the complex causal effects caused by temperature increase (Table 2, Table S1).

5.2. Temperature and light: Ecosystem-level changes

Although there are many studies of climate change impacts on the ecology and physiology of macroalgae, these have often been conducted with single species and under controlled conditions. The eventual outcomes will depend on ecosystem-level responses. Surveys carried out near Finnish and Swedish nuclear power plants have shown that temperature increases, caused by discharge of cooling water, promote excess growth in filamentous algae and increase primary production of the littoral ecosystem (Ilus, 2009; Snoeijs and Prentice, 1989). Under high external nutrient load, this can lead to bottom anoxia, internal loading and eventual destruction of benthic faunal communities. On the other hand, in less eutrophic conditions the impacts of warming were less severe, and the diversity of benthic fauna increased (Ilus, 2009). Near Olkiluoto power plant (West coast of Finland), a rise of mean annual temperature by 2-4 ^{o}C increased abundance of green alga *C. glomerata*, and the *Cladophora* belt formed 2-3 months earlier than in natural conditions (Ilus et al., 1986; Keskitalo and Heitto, 1987). Other species favoured by elevated temperatures were *Enteromorpha ahleriana* (current name *Ulva linza*) and *Ectocarpus siliculosus* (Keskitalo and Ilus, 1987). Interestingly, artificial heating favoured *Ectocarpus siliculosus*, but occurrence of macroscopically similar cold-water species, *Pylaiella littoralis*, was inhibited (Keskitalo and Heitto, 1987; Keskitalo and Ilus, 1987; Snoeijs and Prentice, 1989).

In Sweden, a monitoring survey near a nuclear power plant displayed increased growth, abundance and species diversity of green macroalgae in summer, while red and brown macroalgae declined, except during the winter months (Snoeijs and Prentice, 1989). Overall, the increased temperature and decline of winter ice cover favored opportunistic, short-lived species, which became dominant in the algal communities (Snoeijs and Prentice, 1989).

293 Future warming of the Baltic is coupled with changing light conditions, as the sea ice range and
294 duration decreases (Neumann, 2010) and there is more light available for the onset of growing
295 season in early spring, which may affect phenology of many species (Kraufvelin et al., 2012, 2007).
296 However, the input of organic material into Baltic has been predicted to increase (Meier et al.,
297 2012b) resulting in deteriorating underwater light conditions, which may narrow the macroalgal
298 zones towards the surface, as observed in eutrophic conditions (Kautsky and Kautsky, 1986; Rinne
299 et al., 2011). Increased organic matter increases sedimentation, which impedes macroalgal
300 growth, especially the recruitment of *Fucus* spp. (Eriksson & Johansson, 2003, 2005; Isæus *et al.*,
301 2004, Table 2).

302 *5.3. Responses to low salinity*

303 Based on our literature search, the red algae on average had lowest salinity tolerances, followed by
304 brown algae (Table 2). Green algae contained many species which were very tolerant of low
305 salinities or would actually be expected to benefit from low salinity (Table 2). This pattern is in
306 accordance with physiological tolerance ranges obtained through laboratory experiments (Larsen
307 and Sand-Jensen, 2006) and observed species distributions in field surveys (Bergström and
308 Bergström, 1999).

309 Although Baltic macroalgae have adapted to brackish water, and have generally very high tolerance
310 against low salinity (Larsen and Sand-Jensen, 2006), many species have not been able to inhabit the
311 inner parts of the Baltic Sea (Nielsen et al., 1995; Snoeijs, 1999), and the perennial species of marine
312 origin are absent from regions with lowest salinities (Eriksson and Bergström, 2005). One of the
313 reasons is a failure to reproduce in low salinities. The northern and eastern ranges of *F. vesiculosus*
314 in the Baltic have been suggested to depend on the osmotic tolerance of the gametes (Serrão et al.,
315 1996). At the Gulf of Finland, *F. vesiculosus* is found in salinities down to 3 units (Bäck and

316 Ruuskanen, 2000), at the Swedish coast the distribution limit is at salinity of 4 (Kautsky et al., 1992).
317 *F. radicans* tolerates lower salinity than *F. vesiculosus*, and its distribution in the Bothnian Sea lies
318 in the salinity range of 3 to 5 (Bergström et al., 2005; Leidenberger and Giovanni, 2015). *F. radicans*
319 reproduces asexually in low salinities (Tatarenkov et al., 2005), and the rapid speciation of *F.*
320 *radicans* from *F. vesiculosus* has been attributed to low salinity levels (Pereyra et al., 2009). In *F.*
321 *vesiculosus*, low salinity alters sex ratios, as populations become dominated by female plants in low
322 salinities (Malavenda and Voskoboinikov, 2009). This kind of responses may decrease genetic
323 diversity, and make the local populations more vulnerable to other environmental changes.

324 Although some studies indicate salinities below 4 psu to be harmful *for F. vesiculosus* (Serrão et al.,
325 1999, 1996), field observations have identified persistence of local populations even in salinities
326 down to 2 psu (Ardehed et al., 2016; Munda, 1999; Ruuskanen and Bäck, 2002), with high rates of
327 sexual reproduction (Ardehed et al., 2016). This indicates that local populations may differ in their
328 salinity tolerance, although the size of *F. vesiculosus* plants decreases rapidly with declining salinity
329 (Bäck, 1993; Bäck and Ruuskanen, 2000; Kalvas and Kautsky, 1998; Ruuskanen and Bäck, 1999).

330 Inhibition of sexual reproduction occurs also in other species in low salinities. The abundance of the
331 perennial, coarsely branched red alga *F. lumbricalis* declines with salinity (Bergström and
332 Bergström, 1999) and no sexual reproduction was observed in lowest salinities (3.6 units) sampled
333 (Kostamo and Mäkinen, 2006). The filamentous red alga *C. tenuicorne* has been observed to grow
334 in salinities from 25 to 1 units, and in the lowest salinities asexual reproduction is common
335 (Bergström et al., 2003). Some local populations in the Bothnian Bay have salinity optima as low as
336 1.5 units, but growth is severely reduced in these conditions (Bergström and Kautsky, 2006).

337 Many brown and green algal species in the Baltic can tolerate low salinity reasonably well. The Baltic
338 *P. littoralis* has shown vigorous growth in laboratory in salinity levels of 1.5 units (Russell, 1994),

and also *E. siliculosus* tolerates low salinities (Dittami et al., 2012; Munda, 1999). The filamentous green algae *C. glomerata* is originally a fresh-water species and is expected to be favoured by low salinities (Munda, 1999; Thomas et al., 1990, 1988). *Cladophora rupestris* is of marine origin, and in the Atlantic it grows in the intertidal zone, while in the Baltic it is found in the upper sublittoral. Salinity tolerance of *C. rupestris* is lower than that of *C. glomerata* (Bergström and Bergström, 1999; Thomas et al., 1990, 1988), and thus it is expected to decline with low salinity. Another abundant filamentous green alga *U. intestinalis* showed the highest tolerance for low salinity of 44 macroalgal species studied by Larsen and Sand-Jensen (2006) with no decline in photosynthesis at 0 salinity after 4 days of incubation. As species tolerant of low salinity (Alström-Rapaport et al., 2010; McAvoy and Klug, 2005; Reed and Russell, 1979), *U. intestinalis* extends its distribution throughout the Baltic (Leskinen et al., 2004).

The decrease in number of macroalgal species along the salinity gradient causes a steep decline in the overall biodiversity and biomass of rocky shore communities (Bergström and Bergström, 1999). The ratio of marine to freshwater algal species declines from 4.2 to 1 in the Gulf of Bothnia in a salinity gradient of 5 to 3.5 (Bergström and Bergström, 1999). In the Baltic, there is a decline in red algal (Rhodophyta) and brown algal species (Phaeophyceae) and an increase in green algae (Chlorophyta) along declining salinity (Nielsen et al., 1995; Ojaveer et al., 2010; Snoeijs, 1999), which matches with salinity tolerances derived from experiments (Larsen and Sand-Jensen, 2006), as well as with the results of our literature search (Table 2). The Chlorophyta contain more species of fresh-water origin (Johansson, 2002) with optima in low salinities and even fresh water (Larsen and Sand-Jensen, 2006). In the Bothnian Bay, some macroalgal communities in low salinities are dominated by lacustrine green alga *Cladophora aegagropila,* which extends its distribution down to 10 meters (Bergström and Bergström, 1999).

362 Substantial reductions in biodiversity of marine-associated species with declining salinities have
363 been predicted especially through the loss of fucoids (Vuorinen et al., 2015). Our results suggest
364 that *F. vesiculosus* could potentially show some adaption to low salinities as local populations may
365 have salinity tolerances lower than the generally assumed 4 psu. However, as the size of the plants
366 decreases concurrently with salinity, the ecosystem functions provided by *F. vesiculosus*, such as
367 year-round habitat persistence and complexity, biomass, and nutrient uptake, may be lost or
368 diminished. As an example, *F. radicans* (which could potentially replace *F. vecisulosus* in areas of
369 low salinity in the future), harbors less diverse communities of associated flora and fauna because
370 of smaller size of the thallus (Schagerström et al., 2014).

371 Since many species in Chlorophyta manage well or even prefer low salinity conditions, the
372 macroalgal community in the Baltic may become increasingly dominated by green algae if salinity
373 declines. This would change ecosystem functions and associated species as well, since many green
374 algae are fast-growing, opportunistic annual species, often overwintering as spores, and thus being
375 unable to provide habitat for faunal species during e.g. winters. . The macroalgal beds in the Baltic
376 are important nurseries for fishes and invertebrates (Kautsky et al., 1992), and possible changes
377 would be mediated also to higher trophic levels of pelagic and terrestrial coastal ecosystems
378 through altered energy and nutrient flows.

379 Although potentially some compensation could be gained from colonization by freshwater algal
380 species, these mostly lack large, perennial species. Also, large-scale replacement of marine species
381 by freshwater species under horohalinicum (5 to 8 units) has not been observed with macroalgae
382 (Schubert et al., 2011).

383 *5.4. Ocean acidification and CO_2 fertilization*

384 The macroalgal photosynthesis is mainly C_3-based (Koch et al., 2013) and utilizes RuBisCO, which is
385 the core enzyme in fixing organic carbon (Raven et al., 2008). Diffusion of CO_2 in water is several
386 orders of magnitude lower than in air (Falkowski and Raven, 2007), which means that
387 photoautotrophs may easily become carbon limited, if they only rely on passive diffusion for their
388 carbon acquisition. Most macroalgae use dissolved CO_2 as a source of inorganic carbon (Koch et al.,
389 2013). Carbon uptake by photosynthesis may cause high local fluctuations of pH and depletion of
390 free dissolved CO_2 (Hurd et al., 2009; Middelboe and Hansen, 2007). To overcome this problem,
391 most macroalgae have evolved carbon concentrating mechanisms (CCMs), which increase CO_2
392 concentration at the site of RubisCO activity (Koch et al., 2013; Raven et al., 2008). This may involve
393 active uptake and transport of CO_2 or HCO_3^- (Raven et al., 2008), or secretion of H^+ to enhance
394 dissociation of HCO_3^- to CO_2 (Koch et al., 2013), but with an energetic cost related to the transport,
395 secretion and maintenance/production of the cellular machinery involved (Raven et al., 2014).
396 Species using bicarbonate convert HCO_3^- to CO_2 either using intracellular or periplasmic carbonic
397 anhydrases (CA) or CCMs (Hurd et al., 2009). Many macroalgal species use CCMs facultatively at low
398 CO_2 concentrations (Koch et al., 2013). Species lacking CCMs are often found in high-flow
399 environments, where currents replenish the CO_2 pool near the plant, or in low-light environments,
400 where overall photosynthesis rates are low, and species do not have the energy to utilize CCMs
401 (Koch et al., 2013).

402 Since usage of CCMs is energetically limited (Hurd et al., 2009; Raven et al., 2011), in most
403 macroalgal species studied so far photosynthesis appears unsaturated in current ocean DIC
404 concentrations despite possessing HCO_3^- -based CCMs (Koch et al., 2013). This implies that
405 increasing atmospheric CO_2 concentration could have a positive impact on macroalgal
406 photosynthesis through improved carbon uptake energetics (Raven et al., 2011). However, results

407 from CO_2 enrichment experiments in macroalgae have shown a wide range of responses, possibly
408 relating to different experimental techniques (Hurd et al., 2009).

409 We found only few studies investigating OA effects on Baltic macroalgae. These (Table 2) would
410 indicate, that red algae and potentially green algae, would benefit from OA. As red algae generally
411 grow deeper, they are more reliant on passive CO_2 diffusion (Snoeijs et al., 2002), and thus would
412 benefit more from the increased CO_2 availability, in contrary to species utilizing efficient CCMs,
413 which frequently grow in high irradiances where CO_2 pool may become depleted by photosynthesis
414 (Koch et al., 2013; Middelboe and Hansen, 2007). Red alga *Hildenbrandia rubra*, abundant
415 throughout the Baltic (Nielsen et al., 1995) was one of the few species that dominated the species-
416 impoverished algal community under high CO_2 (pH 6.7) near volcanic vents in the Mediterranean
417 (Porzio et al., 2011), although as *Hildenbrandia* has been suggested to be a subordinate competitor
418 (Kaehler and Williams, 1996), this result may also stem from competitive release rather than direct
419 pH response. A decline from pH 8.1 to 7.8 changed the structure of macroalgal community, which
420 became dominated by few erect leathery species, when turf type algae declined (Porzio et al., 2011).

421 Ocean acidification experiments conducted on Baltic macroalgae have provided mixed results. In a
422 short-term experiment (duration 3 days), Pajusalu *et al.* (2013) found photosynthesis of *U.*
423 *intestinalis* (green) and *F. lumbricalis* (red) to be stimulated by CO_2 addition, while *F. vesiculosus*
424 (brown) showed no response. Of three species studied, *U. intestinalis* showed the highest
425 stimulation by CO_2. In a second 3-days study, Pajusalu et al. (2016) found the fertilization effect on
426 *F. lumbricalis* to depend on interactions with other environmental factors such as temperature and
427 light. Another green alga, *Ulva prolifera*, showed increased vegetative growth when subjected to
428 low salinity and low pH, but at the same time reproductive cell growth declined (Lin et al., 2011). In
429 another study, OA increased photosynthesis (measured as electron transport rate) in *U. prolifera*,

but at the same time caused increased non-photochemical quenching, indicating lower tolerances to high irradiance as energy-dissipating CCM was downregulated in high CO_2 treatment (Liu et al., 2012). If species within green algae genus respond differently to OA, this may change outcome of competitive interactions in the upper littoral zone. For example, more shade-adapted, opportunistic *Ulva procera*, which is frequently observed in the *Cladophora* belt during summer (Choo et al., 2005), secretes H_2O_2, which reduces photosynthesis of competing macroalgae such as *C. glomerata* (Choo et al., 2005), and secretion of such halocarbons depend on temperature and carbon availability (Abrahamsson et al., 2003; Choo et al., 2004).

The brown alga *F. vesiculosus* was the most intensively studied species in our screening with 7 studies found (Table 2, Table S1). These investigations provided contradicting results, some studies indicating no (Pajusalu et al., 2013) or very weak (Werner et al., 2016) response to acidification. Three studies (Al-Janabi et al., 2016b; Gutow et al., 2014; Werner et al., 2016) found negative responses; however, in the last study CO_2 treatment was coupled with elevated temperature, which the authors interpreted to be driving the decline in *Fucus* biomass (Werner et al., 2016). In a 4-week experiment in Helgoland, North Sea, Gutow *et al.* (2014) found that in atmospheric CO_2 of 700 µatm compared to present atmospheric level, *F. vesiculosus* growth was reduced by 10-15 % and the C:N ratio was lower. Two studies (Al-Janabi et al., 2016a; Nygård and Dring, 2008) found potentially beneficial effects. In Kiel Fjord, Southern Baltic Sea, OA was found to increase survival of *F. vesiculosus* germlings in spring and growth during summer, but no interaction with elevated temperatures was observed (Al-Janabi et al., 2016a). In a laboratory setting, increasing DIC content (but with constant pH) in seawater was found to increase growth and photosynthesis in mature *F. vesiculosus* thalli, and effects of DIC were additive with nutrient increase (Nygård and Dring, 2008).

452 The extrapolation of results from laboratory experiments to nature has numerous challenges, and
453 the contradicting results described above may arise from interplay between other environmental
454 variables such as nutrients and light (Celis-Plá et al., 2015; Verspagen et al., 2014). If photosynthesis
455 is limited by nutrient availability, carbon increase in the form of OA would have only minor effect
456 (Verspagen et al., 2014), but if ample nutrients and carbon are provided, photosynthesis should
457 increase, given no light limitation ensues (Verspagen et al., 2014). As light energy is used to convert
458 inorganic carbon to photosynthates, algae may respond to increases in carbon availability by
459 altering photobiological mechanisms. For example, the increased photochemical quenching in *U.*
460 *prolifera* observed by Liu *et al.* (2012), coupled with lower light requirements may indicate that the
461 plant downregulates light utilization as a response to increased carbon availability. Although
462 macroalgae have been proposed to benefit from OA through improved energetics through CCM
463 downregulation (Koch et al., 2013), this may under high irradiances lead to increased
464 photoinhibition, as CCMs acts as a sink for excessive energy (Liu et al., 2012; Wu et al., 2010). Thus,
465 the OA impacts on Baltic macroalgae expectedly will depend on interactions with nutrient and light
466 availability. In general, OA has been observed to have positive effects on photoautotroph growth
467 and photosynthesis under low irradiance, but negative under high irradiance (Gao et al., 2012). If
468 eutrophication will increase in the future Baltic, also underwater light conditions will deteriorate, as
469 increased turbidity is one of the main consequences of eutrophication. Thus to some extent, OA
470 may benefit some species inhabiting the low irradiance environments in the coastal zone, and
471 potentially could counter some of the adverse effects of eutrophication, if macroalgae are able to
472 photosynthesize more efficiently under low irradiance conditions.

473 The coastal ecosystems of the Baltic Sea have naturally high diurnal and seasonal pH fluctuations
474 caused by photosynthesis (Middelboe and Hansen, 2007) and upwelling of CO_2-rich water (Saderne
475 et al. 2013). An upwelling event recorded September 2011 caused pH to decline from 7.7 (day) to

476 7.26 (night) in a macrophyte meadow at Eckenförde Bay, Germany (Saderne et al., 2013). The
477 expected future drop in global ocean pH of 0.4 units by the end of the century (Feely et al., 2009) is
478 in the same order of magnitude as the amplitudes in diurnal pH fluctuations (0.34 units, August and
479 0.3 - 0.4 units, May) observed by Saderne et al. (2013) and Middelboe & Hansen (2007) in the Baltic
480 macrophyte ecosystems. Photosynthesis of several macroalgae, including *Ulva* spp. and *F.*
481 *vesiculosus*, was measured by Middelboe and Hansen (2007) in pH 8 and 9.3 with several DIC
482 concentrations. All species were able to utilize DIC pool more efficiently in lower pH, showing
483 significantly higher rates of photosynthesis.

484 Annual pH fluctuations measured in Baltic macroalgal habitats in Denmark may exceed 1 units
485 (Middelboe and Hansen, 2007). High pH (~9) occur frequently in spring, summer and autumn, when
486 photosynthetic activity removes carbon from seawater, and is contrasted by lower pH values (~8) in
487 winters (Middelboe and Hansen, 2007). The stochastic upwelling of CO_2-rich water may shortly
488 disrupt this pattern (Saderne et al., 2013), and with future climate change, the intensity of such
489 pulses might increase as the deep waters absorb more atmospheric carbon (Omstedt et al., 2012).
490 As seagrass and macroalgal habitats frequently maintain high pH, they may act as sanctuary habitats
491 against ocean acidification, and increase their importance for especially calcifying species and their
492 juvenile stages. The seasonal fluctuations of pH, light and nutrients mediate the effects of ocean
493 acidification on macroalgae and other organisms and should also be taken into consideration when
494 results of ocean acidification laboratory experiments are extrapolated to natural ecosystems.

495 *5.5 Intensifying eutrophication*

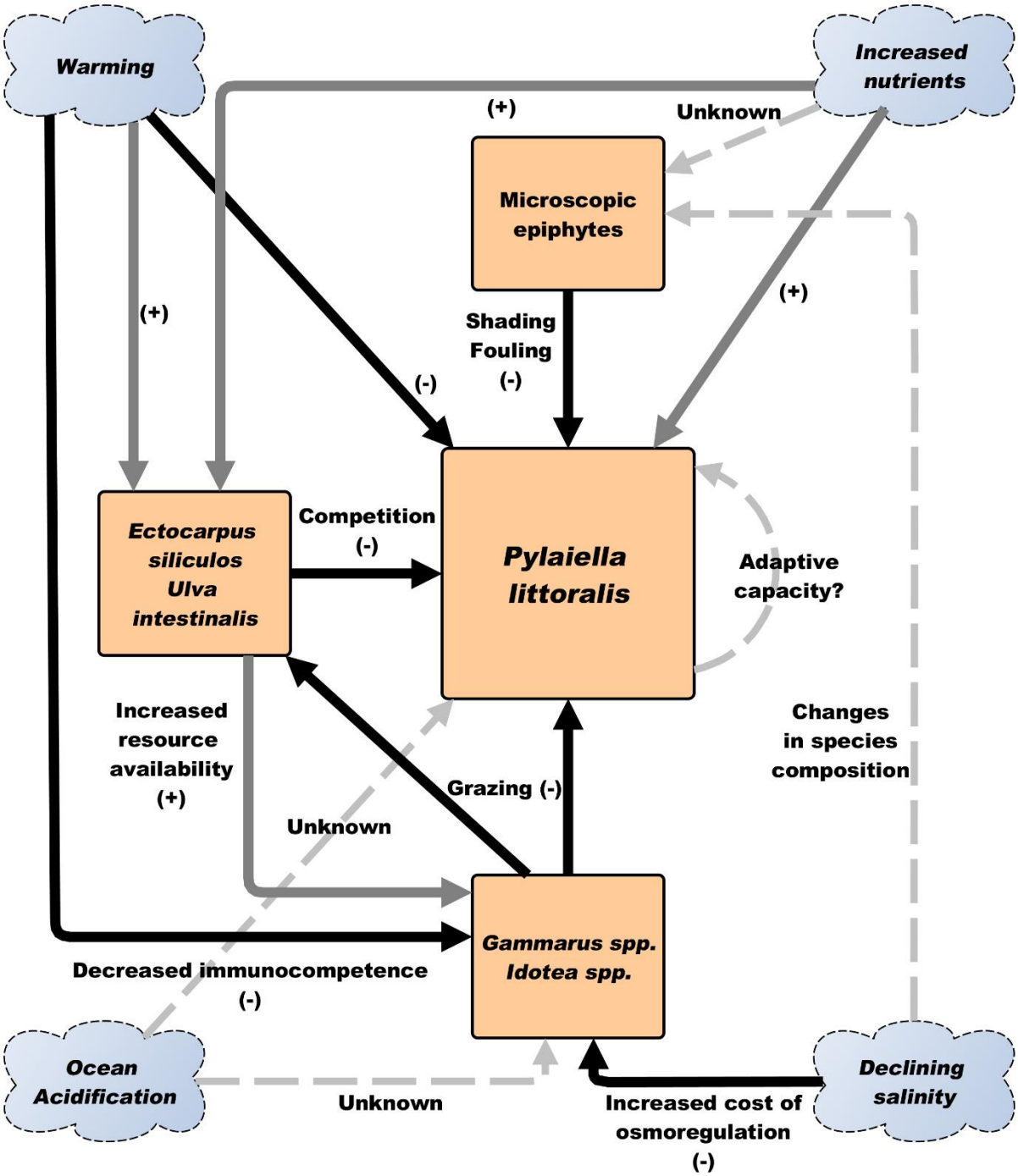
496 As the effects of eutrophication on Baltic macroalgae and coastal ecosystems in general have been
497 covered in different studies in recent decades (Andersen et al., 2017; Kautsky, 1991; Kautsky and
498 Kautsky, 1986; Middelboe and Sand-Jensen, 2000) , we do not address all these effects in detail

here, but only briefly reflect on the results of our literature search. Based on our results, the green algae as a group will clearly benefit from intensifying eutrophication (Table 2, Table S1), together with many red algal species, which, in contrary to our expectations, were quite tolerant against eutrophication and also against subsequent increases in sedimentation. Two brown algae associated with filamentous algae blooms, *P. littoralis* and *E. siliculosus*, showed positive responses. Most of the studies (N = 30) we found quantified either direct or indirect negative effects of eutrophication on the foundation species *F. vesiculosus* (Table 2).

5.6 *Multiple drivers and biotic interactions*

Many studies assessing climate change impacts on marine organisms are short-term and manipulate only one single species and factor of interest (Forsman et al., 2016; Wernberg et al., 2012), often with limited duration (Forsman et al., 2016). In reality, various abiotic components of climate change, such as salinity, temperature, and pH interact influencing the complex biotic community, often under simultaneous non-climatic stressors. Changes in abiotic conditions may alter species interactions leading to rapid changes in abundance. When several abiotic factors change simultaneously, the resulting effects are difficult to predict. We exemplify this with the example of the brown filamentous alga *P. littoralis* (Fig. 2), which frequently forms drifting algal mats. *P. littoralis* seems tolerant to salinity declines (Bergström and Bergström, 1999; Munda, 1999; Russell, 1994), but being a cold-water species might suffer from temperature increases, and in artificially heated areas has been replaced by the sibling species *E. siliculosus* (Keskitalo and Heitto, 1987; Keskitalo and Ilus, 1987). Such declines of *P. littorali*s with increasing temperatures would remove the competitive exclusion pressure on *Ulva* spp. (Lotze et al., 1999), potentially leading to more frequent blooms of *Ulva* spp. in late spring. But *P. littoralis* could also benefit from warming, if ice cover declines result in more light for photosynthesis during early spring when surface water is still

cold. This could shift the peak abundance of *P. littoralis* earlier in spring, which would have important implications for other species, including reproduction and settlement of fucoids and other algae (Berger et al., 2003; Kraufvelin et al., 2007).



526 Figure 2. Interacting climate-change related effects on *Pylaiella littoralis*. Blue boxes indicate climate change related
527 external processes. Gray solid lines indicate positive, black solid lines negative and light gray dashed lines unknown
528 effects.

529

530 We did not find any studies discussing OA effects on *P. littoralis* nor any information regarding its
531 carbon acquisition physiology, so the OA effects remain unknown. *P. littoralis* is strongly favoured
532 by eutrophication (Table 2), and hence increased nutrient input predicted for the future (Meier et
533 al., 2012b) may intensify *P. littoralis* blooms when water temperature remains optimal for the
534 species. Although OA responses could not be identified, it is possible that OA would favor *P. littoralis*
535 in similar way as other species under moderate irradiance (see above). As underwater light
536 environment may further deteriorate by intensifying eutrophication, this kind of conditions may be
537 more abundant in the future.

538 The eventual responses to eutrophication are influenced by grazing (Lotze and Worm, 2000), while
539 grazers themselves are affected by abiotic changes (Hørlyck, 1973; Łapucki and Normant, 2008; Roth
540 et al., 2010). Grazing on *P. littoralis* also intensifies grazing on fucoids as the juveniles thriving on
541 filamentous algae move to feeding on fucoids when reaching adulthood (Orav-Kotta and Kotta,
542 2004). Besides grazing, *P. littoralis* is also affected by shading epiphytes, especially by diatoms which
543 have varying tolerances to salinity (Snoeijs, 1995). *P. littoralis* has nonetheless been shown to have
544 good potential for adaptation to new habitats and changing environmental conditions through
545 emergence of local ecotypes (Bolton, 1979; Russell, 1994), but the evolutionary time required for
546 such changes remains unknown.

547 Similar interacting, synergistic and/or competing effects have been more extensively studied for
548 *Fucus vesiculosus*. For example, increased temperature has been observed to have synergistic

549 effects with low salinity and elevated nutrient concentrations, and may either intensify or decrease
550 grazing pressure (reviewed in Wahl *et al.*, 2011). Experiments with longer exposure times and
551 multiple drivers should be conducted for other key species also, as the existing literature at present
552 seems to be strongly biased on studies on fucoids, more specifically *F. vesiculosus* (Table 2).

553 5.7 *Adaptation*

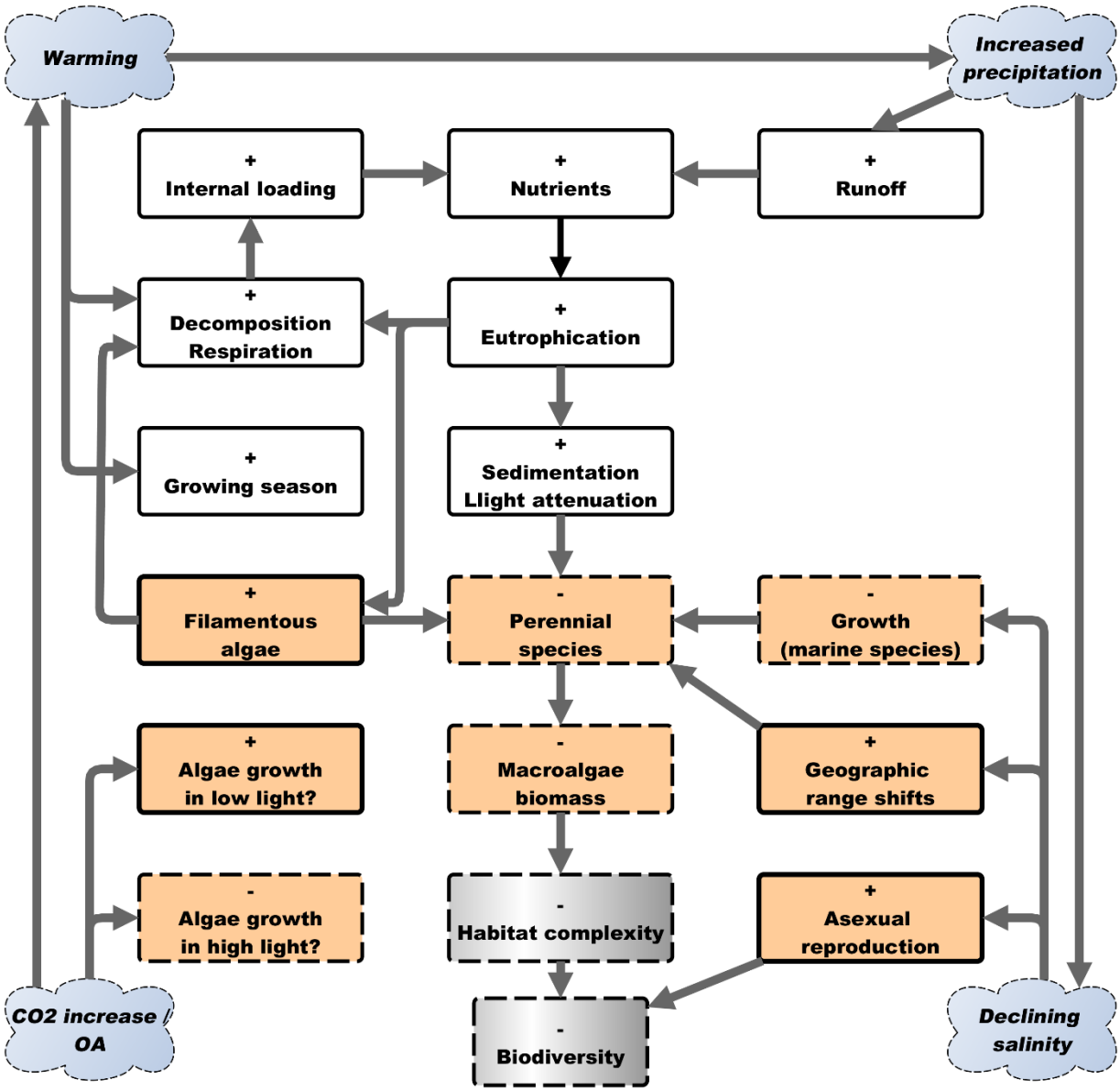
554 When a species is exposed to environmental change, a potential evolutionary change will take
555 several generations. In the context of climate change this may happen rapidly, if there is a strong
556 selection pressure for genotypes carrying suitable alleles (Jump and Penuelas, 2005; Parmesan,
557 2006). Capability of adaptation then depends highly on variation in genes responsible for climate-
558 related traits in any given population (Jump and Penuelas, 2005). Generally, very few examples of
559 genetic adaptation attributed to climate change exists across taxa (Merilä and Hendry, 2014), many
560 adaptive responses in marine organisms being plastic rather than genetic (Collins et al., 2014;
561 Reusch, 2014). Some genetic adaptations to heat (Padfield et al., 2016) and ocean acidification
562 (Lohbeck et al., 2012; Scheinin et al., 2015) have been identified for phytoplankton, but macroalgae
563 with long life-span and generation times are challenging organisms for such studies. However, being
564 sessile organisms macroalgae live in constantly fluctuating environmental conditions and thus
565 possess high intrinsic plasticity (Charrier et al., 2012; Ensminger et al., 2005), which may allow some
566 tolerance against adverse environmental conditions.

567 On one hand bottle necks and founder effects have resulted in overall low genetic variability in Baltic
568 populations (Johannesson et al., 2011), and harsh environmental conditions have resulted in many
569 macroalgae reproducing asexually (Kostamo and Mäkinen, 2006; Tatarenkov et al., 2005). These factors point
570 to low capacity for evolutionary adaption. Yet the Baltic has evolved ecotypes well adapted to local conditions
571 over millennia (Russell, 1985), with subsequent emergence of Baltic ecotypes tolerant of low salinity

572 (Gylle et al., 2009; Johansson et al., 2003; Kostamo et al., 2011; Rueness and Kornfeldt, 1992;
573 Russell, 1994, 1988) and temperature (Nygård and Dring, 2008; Thomas et al., 1988), and also the
574 emergence of an endemic fucoid, *F. radicans*, which has been interpreted as an adaptation to low
575 salinity (Pereyra et al., 2009). Given the speed of observed (Belkin, 2009) and projected (Meier et
576 al., 2012b; Omstedt et al., 2012) environmental change, the potential for similar adaptations in the
577 context of climate change is uncertain. Although some studies on genetic variability in Baltic
578 macroalgae have been conducted (e.g. Leskinen et al. 2004, Tatarenkov et al. 2007), there is very
579 limited knowledge on size of genetic variability related to quantitative traits selected upon in times
580 of rapid environmental change, which makes assessing adaptive capacity difficult.

581 ***6 Conclusions***

582 Summarizing the effects of the different drivers, the combined effects of climate change for
583 macroalgal communities in the Baltic appear similar and additive to those of anthropogenic nutrient
584 increase: elevated primary production and increased abundance of filamentous algae. Climate
585 change will elevate primary production in the littoral ecosystem directly, and through increased
586 nutrient emissions provided by increased river inflow. We illustrate the overall expected responses
587 of macroalgae on abiotic changes in a conceptual model (Fig. 3).



588

589 Figure 3. Conceptual model of expected responses in the macroalgae community. Blue boxes (italics) indicate external
590 climate-change related processes, white boxes indicate responses on the ecosystem level, pink boxes expected
591 responses of the macroalgae community, and gray boxes consequences for other species and the littoral ecosystem.
592 Increases in a process are indicated by + sign and solid box, decreases with - sign and dashed box, respectively.

593

594 Effects of OA on macroalgae remain uncertain, but may potentially increase primary production,
595 especially in red algae. If OA stimulates photosynthesis and growth of phytoplankton (Brading et al.,
596 2011; Sandrini et al., 2016; Scheinin et al., 2015), underwater light conditions could potentially

deteriorate even further from what is expected based on eutrophication scenarios, causing decreased depth penetration of macrophytes. On the other hand, if effects of OA on macroalgal photosynthesis in low light are positive (see above), this may provide some compensation against eutrophication-caused light limitation.

Put together, declining salinity, elevated temperature and increases in nutrient concentrations all strongly favor green, filamentous algae (Table 2). Red algae appear tolerant against eutrophication, but will be negatively affected by low salinity, as they contain more marine species with lower salinity tolerances. Among brown algae, filamentous species such as *E. siliculosus* that benefit from eutrophication, are tolerant against low salinity, and are tolerant or favored by warming, are clearly "future winners", whereas fucoids will likely decline. The reason for this is their low tolerance of eutrophication and mostly harmful direct and indirect effects of warming (Table 2). Although we found some evidence of local population resilience against low salinity, the declining size of individuals, with the loss of genetic diversity in these conditions suggests that for the fucoids the likely outcome isnegative. As they are linked with large number of associated species, their possible decline would have serious biodiversity impacts in coastal ecosystems. Although green algae such as *C. glomerata* may maintain dense faunal populations during summer (Kraufvelin and Salovius, 2004), they lack the year-round persistence of fucoids. Thus through potential loss of foundation species such as *F. vesiculosus*, the structural complexity and annual habitat availability would be severy reduced. If *F. vesiculosus* is lost from the ecosystem, also grazing pressure may intensify on remaining species (Kotta et al., 2000). If green algae proliferate extensively, consequences to benthic fauna are severe as decomposing algae deplete oxygen, leading to severe decreases in faunal abundance, as has been observed in eutrophied conditions (Berezina et al., 2016).

With changes in temperature and salinity conditions, not only the existing interspecific interactions will change, but also the resilience against invasive species, including macroalgae, may diminish in Baltic ecosystems. Invasive species have been identified as one of the major threats to the Baltic ecosystem (Elmgren, 2001). The warmer and less saline conditions in the future may make the Baltic ecosystem more hospitable to a number of potential invaders (Holopainen et al., 2016) especially from estuarine conditions, which could easily transgress the salinity and temperature barriers by traveling via e.g. commercial shipping ballast waters.

Although the temperature and salinity tolerances have been investigated for the most abundant macroalgal species in the context of evolutionary adaptation, the interactions between different drivers have only been studied in fucoids (Wahl et al., 2011) despite the importance of the issue (Koch et al., 2013). In the Baltic Sea the stressors connected to climate change are interacting with eutrophication, hence it is important to investigate the combined effects of salinity, temperature, CO_2 and nutrient concentrations at least on the habitat forming species. In different stages of macroalgal life cycle the environmental conditions may vary widely and this natural variability should be incorporated in the experimental design when planning research campaigns (Wahl et al., 2016). Although in experiments, the projected changes in climatic variables are often simulated through changes in the mean (Boersma et al., 2016), it is frequently extremes that are driving changes in biological systems (Parmesan, 2006). Currently the Baltic macroalgae have to tolerate highly variable biotopes, especially in relation to annual fluctuations in pH and temperature, but the future shifts will likely be accompanied with an increased frequency of climatic events classified as “extreme” (Neumann et al., 2012; Solomon, 2007) exceeding the conditions they are adapted to. Multiple stressors may often cause synergistic effects (Wahl et al., 2011) increasing the likelihood of surpassing a critical tolerance threshold in the future, which should also be considered in planning future research.

643 Very few CO_2 fertilization experiments have been performed on Baltic macroalgae, with mixed
644 results making it hard to extrapolate to the future. Longer experiments (but see Al-Janabi et al.,
645 2016a, 2016b) with well-designed methods for producing the predicted future ocean chemistry
646 (Hurd et al., 2009) should be applied on a wider spectrum of species. In these settings, also other
647 environmental factors such as irradiance, nutrient levels and temperature should be included, as
648 these all may influence the responses of primary producers against OA.

649 The coastal states of the Baltic have limited capacities in stopping or mitigating climate change, and
650 it is therefore important to identify adaptation strategies which maximize the resilience of coastal
651 ecosystems. Since the impacts of climate change intensify those of coastal eutrophication,
652 controlling nutrient emissions is a feasible adaptation strategy in the future, especially since the
653 cost-effectiveness of nutrient emission reductions has been widely studied. As macroalgal beds are
654 environments that can act as buffers against OA as they elevate water pH through photosynthesis
655 (Middelboe and Hansen, 2007), protecting them will also yield benefits for associated species, such
656 as calcifiers, which may be more vulnerable against acidification.

657

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663 **References**

664 Abrahamsson, K., Choo, K.-S., Pedersén, M., Johansson, G., Snoeijs, P., 2003. Effects of temperature on the production
665 of hydrogen peroxide and volatile halocarbons by brackish-water algae. Phytochemistry 64, 725–734.

doi:10.1016/S0031-9422(03)00419-9

Airoldi, L., Balata, D., Beck, M.W., 2008. The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. J. Exp. Mar. Bio. Ecol. 366, 8–15. doi:10.1016/j.jembe.2008.07.034

Al-Janabi, B., Kruse, I., Graiff, A., Karsten, U., Wahl, M., 2016a. Genotypic variation influences tolerance to warming and acidification of early life-stage Fucus vesiculosus L. (Phaeophyceae) in a seasonally fluctuating environment. Mar. Biol. 163, 14. doi:10.1007/s00227-015-2804-8

Al-Janabi, B., Kruse, I., Graiff, A., Winde, V., Lenz, M., Wahl, M., 2016b. Buffering and Amplifying Interactions among OAW (Ocean Acidification & Warming) and Nutrient Enrichment on Early Life-Stage Fucus vesiculosus L. (Phaeophyceae) and Their Carry Over Effects to Hypoxia Impact. PLoS One 11, e0152948. doi:10.1371/journal.pone.0152948

Alström-Rapaport, C., Leskinen, E., Pamilo, P., 2010. Seasonal variation in the mode of reproduction of Ulva intestinalis in a brackish water environment, Aquatic Botany. doi:10.1016/j.aquabot.2010.08.003

Andersen, J.H., Carstensen, J., Conley, D.J., Dromph, K., Fleming-Lehtinen, V., Gustafsson, B.G., Josefson, A.B., Norkko, A., Villnäs, A., Murray, C., 2017. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. Biol. Rev. 92, 135–149. doi:10.1111/brv.12221

Ardehed, A., Johansson, D., Sundqvist, L., 2016. Divergence within and among Seaweed Siblings (Fucus vesiculosus and F. radicans) in the Baltic Sea. PLoS One 11.8, e0161266.

BACC Author Team, 2008. Assessment of climate change for the Baltic Sea basin, Assessment of Climate Change for the Baltic Sea …. Springer, Berlin. doi:10.1007/978-3-540-72786-6

Belkin, I.M., 2009. Rapid warming of Large Marine Ecosystems. Prog. Oceanogr. 81, 207–213. doi:10.1016/j.pocean.2009.04.011

Berezina, N., Gubelit, Y., Polyak, Y., Sharov, A., 2016. An integrated approach to the assessment of the eastern Gulf of Finland health: A case study of coastal habitats. J. Mar. Syst. doi:10.1016/j.jmarsys.2016.08.013

Berger, R., Henriksson, E., Kautsky, L., Malm, T., 2003. Effects of filamentous algae and deposited matter on the survival of Fucus vesiculosus L. germlings in the Baltic Sea. Aquat. Ecol. 37, 1–11. doi:10.1023/A:1022136900630

Bergström, L., Bergström, U., 1999. Species diversity and distribution of aquatic macrophytes in the Northern Quark, Baltic Sea. Nord. J. Bot. 19, 375–383. doi:10.1111/j.1756-1051.1999.tb01131.x

Bergström, L., Bruno, E., Eklund, B., Kautsky, L., 2003. Reproductive Strategies of Ceramium tenuicorne Near Its Inner Limit in the Brackish Baltic Sea. Bot. Mar. 46, 125–131.

Bergström, L., Kautsky, L., 2006. Local adaptation of Ceramium tenuicorne (Ceramiales, Rhodophyta) within the Baltic Sea. J. Phycol. 42, 36–42. doi:10.1111/j.1529-8817.2006.00173.x

Bergström, L., Tatarenkov, A., Johannesson, K., Jönsson, R.B., Kautsky, L., 2005. Genetic and morphological identification of Fucus radicans sp. nov (Fucales, Phaeophyceae) in the brackish Baltic Sea. J. Phycol. 41, 1025–1038.

Boersma, M., Grüner, N., Tasso Signorelli, N., Montoro González, P.E., Peck, M.A., Wiltshire, K.H., 2016. Projecting effects of climate change on marine systems: is the mean all that matters? Proc. R. Soc. London B Biol. Sci. 283.

Bolton, J.J., 1979. ESTUARINE ADAPTATION IN POPULATIONS OF PILAYELLA-LITTORALIS (L) KJELLM (PHAEOPHYTA, ECTOCARPALES). Estuar. Coast. Mar. Sci. 9, 273–280.

Brading, P., Warner, M.E., Davey, P., Smith, D.J., Achterberg, E.P., Suggett, D.J., 2011. Differential effects of ocean acidification on growth and photosynthesis among phylotypes of *Symbiodinium* (Dinophyceae). Limnol. Oceanogr. 56, 927–938. doi:10.4319/lo.2011.56.3.0927

Bučas, M., Daunys, D., Olenin, S., 2007. Overgrowth patterns of the red algae Furcellaria lumbricalis at an exposed Baltic Sea coast: The results of a remote underwater video data analysis. Estuar. Coast. Shelf Sci. 75, 308–316. doi:10.1016/j.ecss.2007.04.038

Bäck, S., 1993. Morphological variation of northern Baltic Fucus vesiculosus along the exposure gradient. Ann. Bot. Fenn. 30, 275–283.

Bäck, S., Collins, J.C., Russell, G., 1992. Effects of salinity on growth of Baltic and Atlantic Fucus vesiculosus. Br. Phycol. J. 27, 39–47. doi:10.1080/00071619200650061

Bäck, S., Ruuskanen, A., 2000. Distribution and maximum growth depth of Fucus vesiculosus along the Gulf of Finland. Mar. Biol. 136, 303–307.

Cameron, A., Askew, N., 2011. EUSeaMap - Preparatory Action for development and assement of European broad-scale habitat map final report.

Celis-Plá, P.S.M., Hall-Spencer, J.M., Horta, P.A., Milazzo, M., Korbee, N., Cornwall, C.E., Figueroa, F.L., 2015. Macroalgal responses to ocean acidification depend on nutrient and light levels. Front. Mar. Sci. 2. doi:10.3389/fmars.2015.00026

Charrier, B., Le Bail, A., de Reviers, B., 2012. Plant Proteus: brown algal morphological plasticity and underlying developmental mechanisms. Trends Plant Sci. 17, 468–477. doi:10.1016/j.tplants.2012.03.003

Choo, K., Nilsson, J., Pedersen, M., 2005. Photosynthesis, carbon uptake and antioxidant defence in two coexisting filamentous green algae under different stress conditions. Mar. Ecol. Prog. Ser. 292, 127–138.

Choo, K., Snoeijs, P., Pedersén, M., 2004. Oxidative stress tolerance in the filamentous green algae Cladophora glomerata and Enteromorpha ahlneriana. J. Exp. Mar. Bio. Ecol. 298, 111–123. doi:10.1016/j.jembe.2003.08.007

Chung, I., Beardall, J., Mehta, S., Sahoo, D., 2011. Using marine macroalgae for carbon sequestration: a critical appraisal. J. Appl. Phycol. 23, 877–86.

Collins, S., Rost, B., Rynearson, T.A., 2014. Evolutionary potential of marine phytoplankton under ocean acidification. Evol. Appl. 7, 140–155. doi:10.1111/eva.12120

Dittami, S.M., Gravot, A., Goulitquer, S., Rousvoal, S., Peters, A.F., Bouchereau, A., Boyen, C., Tonon, T., 2012. Towards deciphering dynamic changes and evolutionary mechanisms involved in the adaptation to low salinities in Ectocarpus (brown algae). Plant J. 71, no-no. doi:10.1111/j.1365-313X.2012.04982.x

Eggert, A., 2012. Seaweed Responses to Temperature, in: Wiencke, C., Bischof, K. (Eds.), Seaweed Biology, Ecological Studies. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 47–66. doi:10.1007/978-3-642-28451-9

Elmgren, R., 2001. Understanding Human Impact on the Baltic Ecosystem: Changing Views in Recent Decades. AMBIO A J. Hum. Environ. 30, 222–231. doi:10.1579/0044-7447-30.4.222

Ensminger, I., Foerster, J., Hagen, C., Braune, W., 2005. Plasticity and acclimation to light reflected in temporal and spatial changes of small-scale macroalgal distribution in a stream. J. Exp. Bot. 56, 2047–58. doi:10.1093/jxb/eri203

Eriksson, B.K., Bergström, L., 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. Estuar. Coast. Shelf Sci. 62, 109–117. doi:10.1016/j.ecss.2004.08.009

Eriksson, B.K., Johansson, G., 2005. Effects of sedimentation on macroalgae: species-specific responses are related to reproductive traits. Oecologia 143, 438–48. doi:10.1007/s00442-004-1810-1

Eriksson, B.K., Johansson, G., 2003. Sedimentation reduces recruitment success of Fucus vesiculosus (Phaeophyceae) in the Baltic Sea. Eur. J. Phycol. 38, 217–222. doi:10.1080/0967026031000121688

Eriksson, B.K., Rubach, A., Hillebrand, H., 2006. BIOTIC HABITAT COMPLEXITY CONTROLS SPECIES DIVERSITY AND NUTRIENT EFFECTS ON NET BIOMASS PRODUCTION. Ecology 87, 246–254. doi:10.1890/05-0090

Falkowski, P., Raven, J., 2007. Aquatic photosynthesis, 2nd ed. Princeton University Press, Princeton.

Feely, R., Doney, S., Cooley, S., 2009. Ocean Acidification: Present Conditions and Future Changes in a High-CO2 World. Oceanography 22, 36–47. doi:10.5670/oceanog.2009.95

Fonselius, S., Valderrama, J., 2003. One hundred years of hydrographic measurements in the Baltic Sea. J. Sea Res. 49, 229–241. doi:10.1016/S1385-1101(03)00035-2

Forsman, A., Berggren, H., Åström, M., Larsson, P., 2016. To What Extent Can Existing Research Help Project Climate Change Impacts on Biodiversity in Aquatic Environments? A Review of Methodological Approaches. J. Mar. Sci. Eng. 4, 75. doi:10.3390/jmse4040075

Fortes, M.D., Lüning, K., 1980. Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. Helgoländer Meeresuntersuchungen 34, 15–29. doi:10.1007/BF01983538

Gao, K., Helbling, E., Häder, D., Hutchins, D., 2012. Responses of marine primary producers to interactions between ocean acidification, solar radiation, and warming. Mar. Ecol. Prog. Ser. 470, 167–189. doi:10.3354/meps10043

Graiff, A., Liesner, D., Karsten, U., Bartsch, I., 2015. Temperature tolerance of western Baltic Sea Fucus vesiculosus – growth, photosynthesis and survival. J. Exp. Mar. Bio. Ecol. 471, 8–16. doi:10.1016/j.jembe.2015.05.009

Gubelit, Y.I., 2015. Climatic impact on community of filamentous macroalgae in the Neva estuary (eastern Baltic Sea). Mar. Pollut. Bull. 91, 166–172. doi:10.1016/j.marpolbul.2014.12.009

767 Gutow, L., Rahman, M.M., Bartl, K., Saborowski, R., Bartsch, I., Wiencke, C., 2014. Ocean acidification affects
768 growth but not nutritional quality of the seaweed Fucus vesiculosus (Phaeophyceae, Fucales). J. Exp. Mar. Bio.
769 Ecol. 453, 84–90. doi:10.1016/j.jembe.2014.01.005

770 Gylle, A., Nygård, C., Ekelund, N., 2009. Desiccation and salinity effects on marine and brackish Fucus vesiculosus
771 L.(Phaeophyceae). Phycologia 48, 156–164.

772 Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D.,
773 Buia, M.-C., 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454, 96–
774 9. doi:10.1038/nature07051

775 HELCOM, 2013. Climate change in the Baltic Sea Area: HELCOM thematic assessment in 2013. Balt. Sea Environ.
776 Proc. No. 137.

777 HELCOM, 2010. Benthic biotope complexes in the Baltic Sea, based on a combination of geological sediment data
778 (BALANCE) and light availability data (EuSeaMap) [WWW Document]. URL http://www.helcom.fi/baltic-sea-
779 trends/data-maps/biodiversity/balance (accessed 1.22.15).

780 Holopainen, R., Lehtiniemi, M., Meier, H.E.M., Albertsson, J., Gorokhova, E., Kotta, J., Viitasalo, M., 2016. Impacts of
781 changing climate on the non-indigenous invertebrates in the northern Baltic Sea by end of the twenty-first
782 century. Biol. Invasions 18, 3015–3032. doi:10.1007/s10530-016-1197-z

783 Hurd, C.L., Hepburn, C.D., Currie, K.I., Raven, J. a., Hunter, K. a., 2009. Testing the effects of ocean acidification on
784 algal metabolism: Considerations for experimental designs. J. Phycol. 45, 1236–1251. doi:10.1111/j.1529-
785 8817.2009.00768.x

786 Hällfors, G., Niemi, Å., Ackefors, H., Lassig, J., Leppäkoski, E., 1981. Biological Oceanography, in: Voipio, A. (Ed.),
787 The Baltic Sea. Elsevier Ltd, Amsterdam, p. 418.

788 Hørlyck, V., 1973. The osmoregulatory ability in three species of the genus Idotea (Isopoda, Crustacea). Ophelia 12,
789 129–140. doi:10.1080/00785326.1973.10430123

790 Ilus, E., 2009. Environmental effects of thermal and radioactive discharges from nuclear power plants in the boreal
791 brackish-water conditions of the northern Baltic Sea. Radiation and Nuclear Safety Authority, Helsinki.

792 Ilus, E., Ojala, J., Sjöblom, K., 1986. Effect of discharges from the Olkiluoto nuclear power station on the receiving
793 waters. Publ Water Res Inst Natl Bd Waters Finl 68, 145–148.

794 Isæus, M., Malm, T., Persson, S., Svensson, A., 2004. Effects of filamentous algae and sediment on recruitment and
795 survival of Fucus serratus (Phaeophyceae) juveniles in the eutrophic Baltic Sea. Eur. J. Phycol. 39, 301–307.
796 doi:10.1080/09670260410001714732

797 Johannesson, K., Smolarz, K., Grahn, M., André, C., 2011. The Future of Baltic Sea Populations: Local Extinction or
798 Evolutionary Rescue? Ambio 40, 179–190. doi:10.1007/s13280-010-0129-x

799 Johansson, G., 2002. Factors Affecting the Distribution of Rocky-Shore Macroalgae on the Swedish coast. Uppsala
800 University.

801 Johansson, G., Sosa, P.A., Snoeijs, P., 2003. Genetic variability and level of differentiation in North Sea and Baltic Sea
802 populations of the green alga Cladophora rupestris. Mar. Biol. 142, 1019–1027. doi:10.1007/s00227-003-1023-x

803 Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J.A., Olsen, J.L., Hoarau, G., 2013. Climate change impact on
804 seaweed meadow distribution in the North Atlantic rocky intertidal. Ecol. Evol. 3, 1356–1373.
805 doi:10.1002/ece3.541

806 Jump, A.S., Penuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change.
807 Ecol. Lett. 8, 1010–1020. doi:10.1111/j.1461-0248.2005.00796.x

808 Kaehler, S., Williams, G., 1996. Distribution of algae on tropical rocky shores: spatial and temporal patterns of non-
809 coralline encrusting algae in Hong Kong. Mar. Biol. 121, 177–187.

810 Kalvas, A., Kautsky, L., 1998. Morphological Variation in Fucus Vesiculosus Populations along Temperature and
811 Salinity Gradients in Iceland. J. Mar. Biol. Assoc. United Kingdom 78, 985–1001.
812 doi:10.1017/S0025315400044921

813 Kautsky, H., 1991. Influence of Eutrophication on the Distribution of Phytobenthic Plant and Animal Communities. Int.
814 Rev. der gesamten Hydrobiol. und Hydrogr. 76, 423–432. doi:10.1002/iroh.19910760315

815 Kautsky, H., Kautsky, L., Kautsky, N., Kautsky, U., Lindblad, C., 1992. Studies on the Fucus vesiculosus community in
816 the Baltic Sea. Acta Phytogeogr. Suec. 78, 33–48.

817 Kautsky, H., Van der Maarel, E., 1990. Multivariate approaches to the variation in phytobenthic communities and

environmental vectors in the Baltic Sea. Mar. Ecol. Prog. Ser. 60, 169–184.

Kautsky, N., Kautsky, H., 1986. Decreased depth penetration of Fucus vesiculosus (L.) since the 1940's indicates eutrophication of the Baltic Sea. Mar. Ecol. Prog. Ser 28, 1–8.

Kautsky, U., 1995. Ecosystem processes in Coastal Areas of the Baltic Sea. Stockholm University.

Keskitalo, J., Heitto, L., 1987. Overwintering of benthic vegetation outside the Olkiluoto nuclear power station, west coast of Finland. Ann. Bot. Fenn. 24, 231–243.

Keskitalo, J., Ilus, E., 1987. Aquatic macrophytes outside the Olkiluoto nuclear power station, west coast of Finland. Ann. Bot. Fenn. 24, 1–21.

Kiirikki, M., 1996. Mechanisms affecting macroalgal zonation in the northern Baltic Sea. Eur. J. Phycol. 31, 225–232. doi:10.1080/09670269600651421

Kiirikki, M., Lehvo, A., 1997. Life Strategies of Filamentous Algae in the Northern Baltic Proper. Sarsia 82, 259–267. doi:10.1080/00364827.1997.10413653

Koch, M., Bowes, G., Ross, C., Zhang, X.-H., 2013. Climate change and ocean acidification effects on seagrasses and marine macroalgae. Glob. Chang. Biol. 19, 103–32. doi:10.1111/j.1365-2486.2012.02791.x

Kostamo, K., Korpelainen, H., Olsson, S., 2011. Comparative study on the population genetics of the red algae Furcellaria lumbricalis occupying different salinity conditions. Mar. Biol. 159, 561–571. doi:10.1007/s00227-011-1835-z

Kostamo, K., Mäkinen, A., 2006. Observations on the mode and seasonality of reproduction in Furcellaria lumbricalis (Gigartinales, Rhodophyta) populations in the northern Baltic Sea. Bot. Mar. 49, 304–309.

Kotta, J., Paalme, T., Martin, G., Makinen, A., 2000. Major changes in macroalgae community composition affect the food and habitat preference of Idotea baltica. Int. Rev. Hydrobiol. 85, 697–705.

Kraufvelin, P., Ruuskanen, A.T., Bäck, S., Russell, G., 2012. Increased seawater temperature and light during early springs accelerate receptacle growth of Fucus vesiculosus in the northern Baltic proper. Mar. Biol. 159, 1795–1807. doi:10.1007/s00227-012-1970-1

Kraufvelin, P., Ruuskanen, A.T., Nappu, N., Kiirikki, M., 2007. Winter colonisation and succession of filamentous macroalgae on artificial substrates and possible relationships to Fucus vesiculosus settlement in early summer. Estuar. Coast. Shelf Sci. 72, 665–674. doi:10.1016/j.ecss.2006.11.029

Kraufvelin, P., Salovius, S., 2004. Animal diversity in Baltic rocky shore macroalgae: can Cladophora glomerata compensate for lost Fucus vesiculosus? Estuar. Coast. Shelf Sci. 61, 369–378. doi:10.1016/j.ecss.2004.06.006

Kuznetsov, I., Neumann, T., 2013. Simulation of carbon dynamics in the Baltic Sea with a 3D model. J. Mar. Syst. 111–112, 167–174. doi:10.1016/j.jmarsys.2012.10.011

Lago-Lestón, A., Mota, C., Kautsky, L., Pearson, G.A., 2009. Functional divergence in heat shock response following rapid speciation of Fucus spp. in the Baltic Sea. Mar. Biol. 157, 683–688. doi:10.1007/s00227-009-1348-1

Łapucki, T., Normant, M., 2008. Physiological responses to salinity changes of the isopod Idotea chelipes from the Baltic brackish waters. Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. 149, 299–305. doi:10.1016/j.cbpa.2008.01.009

Larsen, A., Sand-Jensen, K., 2006. Salt tolerance and distribution of estuarine benthic macroalgae in the Kattegat–Baltic Sea area. Phycologia 45, 13–23. doi:10.2216/03-99.1

Lehmann, A., Getzlaff, K., Harlaß, J., 2011. Detailed assessment of climate variability of the Baltic Sea area for the period 1958-2009. Clim. Res. 46, 185–196.

Lehvo, A., Bäck, S., 2001. Survey of macroalgal mats in the Gulf of Finland, Baltic Sea. Aquat. Conserv. Mar. Freshw. Ecosyst. 11, 11–18. doi:10.1002/aqc.428

Lehvo, A., Bäck, S., Kiirikki, M., 2001. Growth of Fucus vesiculosus L. (Phaeophyta) in the Northern Baltic Proper: Energy and Nitrogen Storage in Seasonal Environment. Bot. Mar. 44, 345–350.

Leidenberger, S., Giovanni, R. De, 2015. Mapping present and future potential distribution patterns for a meso-grazer guild in the Baltic Sea. J. Biogeogr. 42, 241–254.

Leppäranta, M., Myrberg, K., 2009. Physical Oceanography of the Baltic Sea. Springer.

Leskinen, E., Alstrom-Rapaport, C., Pamilo, P., 2004. Phylogeographical structure, distribution and genetic variation of the green algae Ulva intestinalis and U. compressa (Chlorophyta) in the Baltic Sea area. Mol. Ecol. 13, 2257–65. doi:10.1111/j.1365-294X.2004.02219.x

Lin, A.-P., Wang, C., Pan, G.-H., Song, L.-Y., Gao, S., Xie, X.-J., Wang, Z.-Y., Niu, J.-F., Wang, G.-C., 2011. Diluted seawater promoted the green tide of Ulva prolifera (Chlorophyta, Ulvales). Phycol. Res. 59, 295–304. doi:10.1111/j.1440-1835.2011.00629.x

Liu, Y., Xu, J., Gao, K., 2012. CO2 -driven seawater acidification increases photochemical stress in a green alga. Phycologia 51, 562–566. doi:10.2216/11-65.1

Lohbeck, K.T., Riebesell, U., Reusch, T.B.H., 2012. Adaptive evolution of a key phytoplankton species to ocean acidification. Nat. Geosci. 5, 346–351. doi:10.1038/ngeo1441

Lotze, H., Worm, B., 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. Mar. Ecol. Prog. Ser. 200, 167–175. doi:10.3354/meps200167

Lotze, H.K., Schramm, W., Schories, D., Worm, B., 1999. Control of macroalgal blooms at early developmental stages: Pilayella littoralis versus Enteromorpha spp. Oecologia 119, 46–54. doi:10.1007/s004420050759

MacKenzie, B.R., Schiedek, D., 2007. Daily ocean monitoring since the 1860s shows record warming of northern European seas. Glob. Chang. Biol. 13, 1335–1347. doi:10.1111/J.1365-2486.2007.01360.X

Malavenda, S. V., Voskoboinikov, G.M., 2009. Influence of abiotic factors on the structure of the population of the brown alga Fucus vesiculosus in East Murman (Barents Sea). Russ. J. Mar. Biol. 35, 132–137. doi:10.1134/S1063074009020047

Malm, T., Kautsky, L., Engkvist, R., 2001. Reproduction, Recruitment and Geographical Distribution of Fucus serratus L. in the Baltic Sea. Bot. Mar. 44, 101–108.

McAvoy, K.M., Klug, J.L., 2005. Positive and negative effects of riverine input on the estuarine green alga Ulva intestinalis (syn. Enteromorpha intestinalis) (Linneaus). Hydrobiologia 545, 1–9. doi:10.1007/s10750-005-1923-5

Meier, H.E.M., 2006. Baltic Sea climate in the late twenty-first century: a dynamical downscaling approach using two global models and two emission scenarios. Clim. Dyn. 27, 39–68. doi:10.1007/s00382-006-0124-x

Meier, H.E.M., Andersson, H.C., Arheimer, B., Blenckner, T., Chubarenko, B., Donnelly, C., Eilola, K., Gustafsson, B.G., Hansson, A., Havenhand, J., Höglund, A., Kuznetsov, I., MacKenzie, B.R., Müller-Karulis, B., Neumann, T., Niiranen, S., Piwowarczyk, J., Raudsepp, U., Reckermann, M., Ruoho-Airola, T., Savchuk, O.P., Schenk, F., Schimanke, S., Väli, G., Weslawski, J.-M., Zorita, E., 2012a. Comparing reconstructed past variations and future projections of the Baltic Sea ecosystem—first results from multi-model ensemble simulations. Environ. Res. Lett. 7, 34005. doi:10.1088/1748-9326/7/3/034005

Meier, H.E.M., Hordoir, R., Andersson, H.C., Dieterich, C., Eilola, K., Gustafsson, B.G., Höglund, A., Schimanke, S., 2012b. Modeling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961–2099. Clim. Dyn. 39, 2421–2441. doi:10.1007/s00382-012-1339-7

Meier, H.E.M., Kjellström, E., Graham, L.P., 2006. Estimating uncertainties of projected Baltic Sea salinity in the late 21st century. Geophys. Res. Lett. 33, 31–55. doi:10.1029/2006GL026488

Meier, H.E.M., Müller-Karulis, B., Andersson, H.C., Dieterich, C., Eilola, K., Gustafsson, B.G., Höglund, A., Hordoir, R., Kuznetsov, I., Neumann, T., Ranjbar, Z., Savchuk, O.P., Schimanke, S., 2012c. Impact of climate change on ecological quality indicators and biogeochemical fluxes in the Baltic sea: a multi-model ensemble study. Ambio 41, 558–73. doi:10.1007/s13280-012-0320-3

Merilä, J., Hendry, A.P., 2014. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evol. Appl. 7, 1–14. doi:10.1111/eva.12137

Middelboe, A., Hansen, P., 2007. High pH in shallow-water macroalgal habitats. Mar. Ecol. Prog. Ser. 338, 107–117. doi:10.3354/meps338107

Middelboe, A.L., Sand-Jensen, K., 2000. Long-term changes in macroalgal communities in a Danish estuary. Phycologia 39, 245–257. doi:10.2216/i0031-8884-39-3-245.1

Munda, I.M., 1999. The benthic algal vegetation of land-locked fjords in southeastern Iceland. Hydrobiologia 393, 169–180. doi:10.1023/A:1003565309759

Müller, R., Laepple, T., Bartsch, I., Wiencke, C., 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. Bot. Mar. 52, 617–638.

Myrberg, K., Leppäranta, M., Kuosa, H., 2006. Itämeren fysiikka, tila ja tulevaisuus. Yliopistopaino Kustannus, Helsinki.

Neumann, T., 2010. Climate-change effects on the Baltic Sea ecosystem: A model study. J. Mar. Syst. 81, 213–224. doi:10.1016/j.jmarsys.2009.12.001

Neumann, T., Eilola, K., Gustafsson, B., Müller-Karulis, B., Kuznetsov, I., Meier, H.E.M., Savchuk, O.P., 2012. Extremes of temperature, oxygen and blooms in the Baltic sea in a changing climate. Ambio 41, 574–85. doi:10.1007/s13280-012-0321-2

Nicastro, K.R., Zardi, G.I., Teixeira, S., Neiva, J., Serrão, E. a, Pearson, G. a, 2013. Shift happens: trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga Fucus vesiculosus. BMC Biol. 11, 6. doi:10.1186/1741-7007-11-6

Nielsen, R., Kristiansen, A., Mathiesen, L., Mathiesen, H., 1995. Distribution index of the benthic macroalgae of the Baltic Sea area. Acta Bot. Fenn. 155, 55.

Norkko, A., Bonsdorff, E., 1996. Population responses of coastal zoobenthos to stress induced by drifting algal mats. Mar. Ecol. Prog. Ser. 140, 141–151.

Norman, M., Raj Parampil, S., Rutgersson, A., Sahlée, E., 2013. Influence of coastal upwelling on the air–sea gas exchange of CO 2 in a Baltic Sea Basin. Tellus B 65. doi:10.3402/tellusb.v65i0.21831

Nygård, C. a., Dring, M.J., 2008. Influence of salinity, temperature, dissolved inorganic carbon and nutrient concentration on the photosynthesis and growth of Fucus vesiculosus from the Baltic and Irish Seas. Eur. J. Phycol. 43, 253–262. doi:10.1080/09670260802172627

Ojaveer, H., Jaanus, A., Mackenzie, B.R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M.L., Zaiko, A., 2010. Status of biodiversity in the Baltic Sea. PLoS One 5, e12467. doi:10.1371/journal.pone.0012467

Omstedt, A., Edman, M., Anderson, L.G., Laudon, H., 2010. Factors influencing the acid-base (pH) balance in the Baltic Sea: a sensitivity analysis. Tellus B 62, 280–295. doi:10.1111/j.1600-0889.2010.00463.x

Omstedt, A., Edman, M., Claremar, B., Frodin, P., Gustafsson, E., Humborg, C., Hägg, H., Mörth, M., Rutgersson, A., Schurgers, G., Smith, B., Wällstedt, T., Yurova, A., 2012. Future changes in the Baltic Sea acid–base (pH) and oxygen balances. Tellus B 64. doi:10.3402/tellusb.v64i0.19586

Omstedt, A., Gustafsson, E., Wesslander, K., 2009. Modelling the uptake and release of carbon dioxide in the Baltic Sea surface water. Cont. Shelf Res. 29, 870–885. doi:10.1016/j.csr.2009.01.006

Orav-Kotta, H., Kotta, J., 2004. Food and habitat choice of the isopod Idotea baltica in the northeastern Baltic Sea. Hydrobiologia 514, 79–85. doi:10.1023/B:hydr.0000018208.72394.09

Padfield, D., Yvon-Durocher, G., Buckling, A., 2016. Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton. Ecol. Lett. 19, 133–142.

Pajusalu, L., Martin, G., Paalme, T., Põllumäe, A., 2016. The effect of CO2 enrichment on net photosynthesis of the red alga Furcellaria lumbricalis in a brackish water environment. PeerJ 4.

Pajusalu, L., Martin, G., Põllumäe, A., Paalme, T., 2013. Results of laboratory and field experiments of the direct effect of increasing CO2 on net primary production of macroalgal species in brackish-water ecosystems. Proc. Est. Acad. Sci. 62, 148. doi:10.3176/proc.2013.2.09

Parmesan, C., 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100

Pereyra, R.T., Bergström, L., Kautsky, L., Johannesson, K., 2009. Rapid speciation in a newly opened postglacial marine environment, the Baltic Sea. BMC Evol. Biol. 9, 70. doi:10.1186/1471-2148-9-70

Porzio, L., Buia, M.C., Hall-Spencer, J.M., 2011. Effects of ocean acidification on macroalgal communities. J. Exp. Mar. Bio. Ecol. 400, 278–287. doi:10.1016/j.jembe.2011.02.011

Raven, J.A., Beardall, J., Giordano, M., 2014. Energy costs of carbon dioxide concentrating mechanisms in aquatic organisms. Photosynth. Res. 121, 111–24. doi:10.1007/s11120-013-9962-7

Raven, J.A., Cockell, C.S., De La Rocha, C.L., 2008. The evolution of inorganic carbon concentrating mechanisms in photosynthesis. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 363, 2641–50. doi:10.1098/rstb.2008.0020

Raven, J. a, Giordano, M., Beardall, J., Maberly, S.C., 2011. Algal and aquatic plant carbon concentrating mechanisms in relation to environmental change. Photosynth. Res. 109, 281–96. doi:10.1007/s11120-011-9632-6

Reed, R.H., Russell, G., 1979. Adaptation to salinity stress in populations of Enteromorpha intestinalis (L.) Link. Estuar. Coast. Mar. Sci. 8, 251–258. doi:10.1016/0302-3524(79)90095-1

Reusch, T.B.H., 2014. Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. Evol. Appl. 7, 104–122. doi:10.1111/eva.12109

Rinne, H., Salovius-Laurén, S., Mattila, J., 2011. The occurrence and depth penetration of macroalgae along environmental gradients in the northern Baltic Sea. Estuar. Coast. Shelf Sci. 94, 182–191.

doi:10.1016/j.ecss.2011.06.010

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., Imeson, A., 2008. Attributing physical and biological impacts to anthropogenic climate change. Nature 453, 353–7. doi:10.1038/nature06937

Roth, O., Kurtz, J., Reusch, T.B.H., 2010. A summer heat wave decreases the immunocompetence of the mesograzer, Idotea baltica. Mar. Biol. 157, 1605–1611. doi:10.1007/s00227-010-1433-5

Rueness, J., Kornfeldt, R., 1992. Ecotypic differentiation in salinity responses of Ceramium strictum (Rhodophyta) from Scandinavian waters. Sarsia 77, 207–212.

Russell, G., 1994. A Baltic variant of Pilayella littoralis (Algae, Fucophyceae). Ann. Bot. Fenn. 31, 127–138.

Russell, G., 1988. The seaweed flora of a young semi-enclosed sea: The Baltic. Salinity as a possible agent of flora divergence. Helgoländer Meeresuntersuchungen 42, 243–250.

Russell, G., 1985. Recent evolutionary changes in the algae of the Baltic Sea. Br. Phycol. J. 20, 87–104. doi:10.1080/00071618500650111

Ruuskanen, A., Bäck, S., 2002. Morphological changes in submerged Fucus vesiculosus (L) (Phaeophyta) along the salinity gradient of the River Keret estuary, Russia. Sarsia 87, 185–188. doi:10.1080/003648202320205265

Ruuskanen, A., Bäck, S., 1999. Morphological variation of northern Baltic Sea Fucus vesiculosus L. Ophelia 50, 43–59. doi:10.1080/00785326.1999.10409388

Saderne, V., Fietzek, P., Herman, P.M.J., 2013. Extreme variations of pCO2 and pH in a macrophyte meadow of the Baltic Sea in summer: evidence of the effect of photosynthesis and local upwelling. PLoS One 8, e62689. doi:10.1371/journal.pone.0062689

Sandrini, G., Ji, X., Verspagen, J.M.H., Tann, R.P., Slot, P.C., Luimstra, V.M., Schuurmans, J.M., Matthijs, H.C.P., Huisman, J., 2016. Rapid adaptation of harmful cyanobacteria to rising CO_2. Proc. Natl. Acad. Sci. 201602435. doi:10.1073/pnas.1602435113

Schagerström, E., Forslund, H., Kautsky, L., Pärnoja, M., Kotta, J., 2014. Does thalli complexity and biomass affect the associated flora and fauna of two co-occurring Fucus species in the Baltic Sea? Estuar. Coast. Shelf Sci. 149, 187–193. doi:10.1016/j.ecss.2014.08.022

Scheinin, M., Riebesell, U., Rynearson, T.A., Lohbeck, K.T., Collins, S., 2015. Experimental evolution gone wild. J. R. Soc. Interface 12, 457–469. doi:10.1098/rsif.2015.0056

Schubert, H., Feuerpfeil, P., Marquardt, R., Telesh, I., Skarlato, S., 2011. Macroalgal diversity along the Baltic Sea salinity gradient challenges Remane's species-minimum concept. Mar. Pollut. Bull. 62, 1948–56. doi:10.1016/j.marpolbul.2011.06.033

Seitzinger, S.P., Kroeze, C., Bouwman, A.F., Caraco, N., Dentener, F., Styles, R. V., 2002. Global patterns of dissolved inorganic and particulate nitrogen inputs to coastal systems: Recent conditions and future projections. Estuaries 25, 640–655. doi:10.1007/BF02804897

Serrão, E.A., Brawley, S.H., Hedman, J., Kautsky, L., Samuelsson, G., 1999. REPRODUCTIVE SUCCESS OF FUCUS VESICULOSUS (PHAEOPHYCEAE) IN THE BALTIC SEA. J. Phycol. 35, 254–269. doi:10.1046/j.1529-8817.1999.3520254.x

Serrão, E.A., Kautsky, L., Brawley, S.H., 1996. Distributional success of the marine seaweed Fucus vesiculosus L. in the brackish Baltic Sea correlates with osmotic capabilities of Baltic gametes. Oecologia 107, 1–12. doi:10.1007/BF00582229

Siegel, H., Gerth, M., Tschersich, G., 2006. Sea surface temperature development of the Baltic Sea in the period 1990-2004. Oceanologia 48, 119–131.

Snoeijs, P., 1999. 12. Marine and brackish waters. Acta Phytogeogr. Suec. 84, 187–212.

Snoeijs, P., 1995. Effects of salinity on epiphytic diatom communities on Pilayella littoralis (Phaeophyceae) in the Baltic Sea. Ecoscience 2, 382–394. doi:10.1080/11956860.1995.11682307

Snoeijs, P., Klenell, M., Choo, K., Comhaire, I., Ray, S., Peders, M., 2002. Strategies for carbon acquisition in the red marine macroalga Coccotylus truncatus from the Baltic Sea. Mar. Biol. 140, 435–444. doi:10.1007/s00227-001-0729-x

Snoeijs, P.J.M., Prentice, I.C., 1989. Effects of cooling water discharge on the structure and dynamics of epilithic algal communities in the northern Baltic. Hydrobiologia 184, 99–123. doi:10.1007/BF00014306

Solomon, S., 2007. Climate change 2007-the physical science basis: Working group I contribution to the fourth

assessment report of the IPCC. Cambridge University Press.

Tatarenkov, A., Bergström, L., Jönsson, R.B., Serrão, E.A., Kautsky, L., Johannesson, K., 2005. Intriguing asexual life in marginal populations of the brown seaweed Fucus vesiculosus. Mol. Ecol. 14, 647–51. doi:10.1111/j.1365-294X.2005.02425.x

Tatarenkov, A., Jönsson, R.B., Kautsky, L., Johannesson, K., 2007. GENETIC STRUCTURE IN POPULATIONS OF FUCUS VESICULOSUS (PHAEOPHYCEAE) OVER SPATIAL SCALES FROM 10 M TO 800 KM 1. J. Phycol. 43, 675–685. doi:10.1111/j.1529-8817.2007.00369.x

Thomas, D.N., Collins, J.C., Russell, G., 1990. Interpopulation differences in the salt tolerance of two Cladophora species. Estuar. Coast. Shelf Sci. 30, 201–206. doi:10.1016/0272-7714(90)90064-X

Thomas, D.N., Collins, J.C., Russell, G., 1988. Interactive Effects of Temperature and Salinity upon Net Photosynthesis of Cladophora glomerata (L.) Kütz. and C. rupestris (L.) Kütz. Bot. Mar. 31. doi:10.1515/botm.1988.31.1.73

Verspagen, J.M.H., Van de Waal, D.B., Finke, J.F., Visser, P.M., Huisman, J., 2014. Contrasting effects of rising CO2 on primary production and ecological stoichiometry at different nutrient levels. Ecol. Lett. 17, 951–60. doi:10.1111/ele.12298

Vuorinen, I., Hänninen, J., Rajasilta, M., Laine, P., Eklund, J., Montesino-Pouzols, F., Corona, F., Junker, K., Meier, H.E.M., Dippner, J.W., 2015. Scenario simulations of future salinity and ecological consequences in the Baltic Sea and adjacent North Sea areas-implications for environmental monitoring. Ecol. Indic. 50, 196–205. doi:10.1016/j.ecolind.2014.10.019

Waern, M., 1952. Rocky-shore algae in the Oregrund archipelago. Almqvist & Wiksells Boktr., Uppsala.

Wahl, M., Jormalainen, V., Eriksson, B.K., Coyer, J.A., Molis, M., Schubert, H., Dethier, M., Karez, R., Kruse, I., Lenz, M., Pearson, G., Rohde, S., Wikström, S.A., Olsen, J.L., 2011. Stress ecology in fucus: abiotic, biotic and genetic interactions. Adv. Mar. Biol. 59, 37–105. doi:10.1016/B978-0-12-385536-7.00002-9

Wahl, M., Saderne, V., Sawall, Y., 2016. How good are we at assessing the impact of ocean acidification in coastal systems? Limitations, omissions and strengths of commonly used experimental approaches with special emphasis on the neglected role of fluctuations. Mar. Freshw. Res. 67, 25–36. doi:10.1071/MF14154

Wernberg, T., Russell, B.D., Thomsen, M.S., Gurgel, C.F.D., Bradshaw, C.J.A., Poloczanska, E.S., Connell, S.D., 2011. Seaweed Communities in Retreat from Ocean Warming, Current Biology. doi:10.1016/j.cub.2011.09.028

Wernberg, T., Smale, D. a., Thomsen, M.S., 2012. A decade of climate change experiments on marine organisms: procedures, patterns and problems. Glob. Chang. Biol. 18, 1491–1498. doi:10.1111/j.1365-2486.2012.02656.x

Werner, F.J., Graiff, A., Matthiessen, B., 2016. Even moderate nutrient enrichment negatively adds up to global climate change effects on a habitat-forming seaweed system. Limnol. Oceanogr. 61, 1891–1899. doi:10.1002/lno.10342

Wiencke, C., Bartsch, I., Bischoff, B., Peters, A.F., Breeman, A.M., 1994. Temperature Requirements and Biogeography of Antarctic, Arctic and Amphiequatorial Seaweeds. Bot. Mar. 37, 247–260. doi:10.1515/botm.1994.37.3.247

Winsor, P., Rodhe, J., Omstedt, A., 2001. Baltic Sea ocean climate : an analysis of 100 yr of hydrographic data with focus on the freshwater budget. Clim. Res. 18, 5–15.

Wu, Y., Gao, K., Riebesell, U., 2010. CO2-induced seawater acidification affects physiological performance of the marine diatom Phaeodactylum tricornutum. Biogeosciences (BG) 7, 2915–2923.